

**THE LATE MIOCENE DOLPHIN *PITHANODELPHIS* ABEL,
1905 (CETACEA: KENTRIODONTIDAE)
FROM CALIFORNIA**

Lawrence G. Barnes¹

ABSTRACT. Fossil species of the unusual and relatively highly derived kentriodontid dolphin genus *Pithanodelphis* Abel, 1905, are now known from rocks bordering both the North Atlantic and the North Pacific Ocean basins. The type species of this genus, Late Miocene *Pithanodelphis cornutus* (du Bus, 1872), is known from the Antwerp Basin in Belgium. A skull illustrated by Abel in 1905 is here designated as the lectotype of this species. An approximately contemporaneous species, *Pithanodelphis nasalis*, new species, differs from *P. cornutus* by having a different suite of derived and primitive cranial characters and it is one of the most abundant fossil cetaceans in the Late Miocene age Monterey and Modelo formations in southern California.

Bones around the nares and cranial vertex of species of *Pithanodelphis* are asymmetrical, but in a unique manner that is totally unlike the condition in species of modern Delphinidae and other Odontoceti which possess cranial asymmetry. The nasal bones are very large. In recognition of these derived characters, *Pithanodelphis* is classified in a new subfamily of Kentriodontidae, the Pithanodelphininae. Apparently *Pithanodelphis nasalis* was able to produce sounds used for echolocation, lived in moderately deep water offshore over the continental shelf, and had a heterogeneous diet comprised mostly of small fishes. Adult individuals attained a body length of approximately 200 cm. The vertebral column is similar to those of the Middle Miocene fossil kentriodontine dolphin, *Delphinodon dividuum* True, 1912b, and the extant bottlenosed dolphin, *Tursiops truncatus* Montagu, 1821.

INTRODUCTION

Recent studies have shown that during Miocene time an extinct group of dolphins, the family Kentriodontidae, which was first recognized from fossils found in deposits around the North Atlantic Ocean, also had an equally significant history in the North Pacific Ocean (Barnes, 1977, 1978; Barnes and Mitchell, 1984). Five kentriodontid genera are now known to have had species that lived in both ocean basins, and one of these is the genus *Pithanodelphis* Abel, 1905. The type

species of the genus is *P. cornutus* (du Bus, 1872), which is known only from specimens found in Late Miocene sediments in the Antwerp Basin in Belgium. I have previously (Barnes, 1977) recognized the genus *Pithanodelphis* from the approximately correlative Monterey Formation in southern California, and classified the genus in the nominate kentriodontid subfamily Kentriodontinae (Barnes, 1978).

The fossils from California represent a new species that I described in a Ph.D. dissertation (Barnes, 1972). This species is known by several skulls and some postcranial bones, most of which are from a vertically and laterally restricted stratigraphic section of the Monterey Formation in the San Joaquin Hills in Orange County, California, near the southern limit of the topographic and depositional feature known as the Los Angeles Basin (Woodford et al., 1954). Some of the fossils were discovered in naturally formed outcrops, but most were discovered in 1969 as a result of earth-moving for construction of an extensive commercial/manufacturing complex for North American Rockwell Land Corporation near Aliso Creek in the Laguna Niguel district, part of which later became the offices of the United States General Services Administration. This site has been discussed by Domning (1978), Howard (1978), and Barnes, Raschke, and McLeod (in press). One additional specimen that I refer to this species is from the correlative Upper Member of the Modelo Formation that is exposed 84 km to the north of Laguna Niguel in the Santa Monica Mountains, Los Angeles County, California. The purpose of this paper is to diagnose these fossils as a new species and to describe the available sample of specimens.

1. Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.

METHODS AND MATERIALS

In this study, the closest comparisons are made between the new species and two other kentriodontids. I refer the reader to descriptions and illustrations of specimens of *Kentriodon pernix* Kellogg, 1927, provided by Kellogg (1927, 1928), Barnes (1978, including other species of kentriodontids), and Barnes and Mitchell (1984), and of *Delphinodon dividum* True, 1912b, provided by True (1912b), Barwick (1939), and Barnes (1978). I have also made comparisons with various living odontocete taxa. Systematics and ranges of these are provided by Hershkovitz (1966) and Rice (1984).

Measurements of skulls and the mandible were made following the methods outlined by Perrin (1975). In the tables of measurements, a number in parentheses following the description of a parameter refers to the same measurement of Perrin. Anatomical terminology is derived from Kellogg (1927), Fraser and Purves (1960), Kasuya (1973), Barnes (1978, 1984), and Barnes and Mitchell (1984). The repository of specimens, the Natural History Museum of Los Angeles County, Los Angeles, California, is abbreviated LACM. Precise locality descriptions may be provided to qualified investigators upon request.

In the illustrations, bones and other anatomical structures are labeled according to the following abbreviations:

aon—antorbital notch
Bo—basioccipital bone
Bs—basisphenoid bone
ch—cranial hiatus
eam—external acoustic meatus
fio—ventral apertures, infraorbital foramen
fmx—maxillary foramen
fop—optic foramen
fpal—palatine foramen
fpmx—premaxillary foramen
Fr—frontal bone
gf—glenoid fossa
Ju—jugal bone
La—lacrimal bone
Met—mesethmoid bone
mrg—mesorostral gutter
ms—middle sinus
Mx—maxillary bone
n—naris
Na—nasal bone
Oc—occipital bone
occ—occipital condyle
Pa—parietal bone
Pal—palatine bone
Pmx—premaxillary bone
pop—paroccipital process
Pt—pterygoid bone
Pt(l)—lateral lamina of pterygoid
Pt(ml)—medial lamina of pterygoid
pts—fossa for pterygoid sinus
sq—squamosal bone

sqf—squamosal fossa
Vo—vomer bone

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Superfamily Delphinoidea (Gray, 1821)
Flower, 1864

Family Kentriodontidae (Slijper, 1936)
Barnes, 1978

Kentriodontinae Slijper, 1936:556; as a subfamily of the family Delphinidae.

Kentriodontidae. Slijper, 1958:label in fig. 36; emended rank without explanation in text.

Kentriodontidae. Barnes, 1978:3; emended rank, as a family of the superfamily Delphinoidea.

EMENDED DIAGNOSIS OF FAMILY. A family in the superfamily Delphinoidea differing from Albireonidae, Monodontidae, Delphinidae, and Phocoenidae by having skulls with small pterygoid sinus in pterygoid hamulus; differing from Monodontidae, Delphinidae, and Phocoenidae by lacking excavation in exoccipital for posterior sinus and in lateral side of basioccipital for peribullary and/or pterygoid sinus, by having symmetrical posterior ends of premaxillae which contact nasals on both right and left sides, and by having symmetrical cranial vertex (except in case of kentriodontids with asymmetrical vertex, which have midline between nasals twisted to right instead of to left); differing from Delphinidae and Phocoenidae by lacking anterior sinus and lacking large posterodorsal extension of antorbital lobe of pterygoid sinus between frontal and maxilla; differing from Albireonidae and Phocoenidae by lacking premaxillary eminences and having instead, wide, flat, and elevated spiracular plates on premaxillae on either side of external nares; differing from Monodontidae and Delphinidae by having symmetrical mesethmoid and external nares, equal areas of vertex covered by right and left nasals, and by having right and left spiracular plates approximately equal in size; and differing from Albireonidae by having mesorostral gutter open dorsally.

INCLUDED SUBFAMILIES. Kampholophinae Barnes, 1978; Kentriodontinae (Slijper, 1936) Barnes, 1978; Lophocetinae Barnes, 1978; and Pithanodelphinae, new subfamily.

Subfamily Pithanodelphinae, new subfamily

DIAGNOSIS OF SUBFAMILY. A subfamily of Kentriodontidae differing from Kampholophinae, Lophocetinae, and Kentriodontinae by having skulls with asymmetrical cranial vertex in which midline between nasals bends toward right side posteriorly, right maxilla encroaches farther than left toward midline posteriorly, right spiracular plate is slight-

ly wider than left, and right nasal is higher than left, posterior end of premaxilla extending as slender projection between nasal and maxilla rather than wide, abruptly terminating and with elevated posterolateral corner, nasal bone much larger and very convex, olfactory fontanelle present in posterior wall of each naris; differing further from Kampholophinae and Kentriodontinae by having periotic with narrower, more transversely compressed anterior process; and differing further from Kentriodontinae by lacking obliquely oriented sulcus on anterolateral surface of nasal bone within upper part of naris.

TYPE AND ONLY INCLUDED GENUS. *Pithanodelphis* Abel, 1905, Late Miocene, Belgium and California.

Pithanodelphis Abel, 1905

Phocaenopsis Huxley, 1859, part. du Bus, 1872:500.

Pithanodelphis Abel, 1905:142; for *Phocaenopsis cornutus* du Bus, 1872, only.

EMENDED DIAGNOSIS OF GENUS. The same as for the subfamily until other genera are assigned to the subfamily.

TYPE SPECIES. *Pithanodelphis cornutus* (du Bus, 1872).

INCLUDED SPECIES. *Pithanodelphis cornutus* (du Bus, 1872); and *Pithanodelphis nasalis*, new species.

Pithanodelphis nasalis, new species

Figures 1-14

aff. *Pithanodelphis* Abel, 1905. Barnes, 1977:328 (table 4).

DIAGNOSIS OF SPECIES. A species of *Pithanodelphis* differing from *P. cornutus* by having skull with more prominent lambdoidal and occipital crests, occipital shield smaller and not as convex, temporal fossa curving farther around margin of occipital shield, nasal relatively larger, zygomatic process of squamosal smaller with more tapered anterior end.

HOLOTYPE. LACM 30093, a nearly complete skull, dorsoventrally crushed, lacking much of the basicranium, bearing 23 whole or incomplete teeth in place, with 16 loose teeth, right and left tympanic bullae, left periotic, malleus, incus, and stapes; right and left dentaries with 11 whole or partial teeth in place, collected by W. Earl Calhoun and Michael K. Hammer in 1969.

TYPE LOCALITY. LACM locality 5077, Laguna Niguel district, San Joaquin Hills, Orange County, California.

PARATYPES. LACM 26635, an undistorted but badly shattered incomplete skull lacking anterior end of the rostrum and basicranium, bearing five whole or partial teeth in place, and one fragment of the extremity of the rostrum, collected at LACM locality 5069 by W. Earl Calhoun in 1969. LACM 29087, two fragments of a skull (the dorsolateral corner of the braincase and the left squamosal), partial vertebral column and ribs, collected at LACM locality 5082 by Marion J. Bohrer and W. Earl Calhoun in 1969.

REFERRED SPECIMENS FROM THE MONTEREY FORMATION. LACM 31186, right side of rostrum col-

lected at LACM locality 5071 by Marion J. Bohrer in 1969; LACM 122670, left periotic collected by Michael D. Quarles, 8 November 1982, and LACM 123872, skull, collected by David P. Whistler and L.G. Barnes, 31 May 1975, both from LACM locality 6902; LACM 123873, skull collected at LACM locality 1101 by Michael K. Hammer.

FORMATION AND AGE. The holotype, paratypes, and referred specimens listed above are all from rocks that have been identified as the upper part of the Monterey Formation (Vedder, Yerkes, and Schoellhamer, 1957; Fife, 1974), correlated with the "Margaritan" provisional mega-invertebrate stage of Addicott (1972), with the Mohnian foraminiferal stage, and indirectly with the later part of the Clarendonian North American land mammal age, and are of Late Miocene age, approximately 10 to 11 million years old (Barnes, 1977; Repenning and Tedford, 1977; Howard, 1978). This part of the Monterey Formation has yielded a diverse fossil vertebrate assemblage (Barnes, Raschke, and McLeod, in press), including the bird fossils that were described by Howard (1976, 1978), the sirenian fossils reported by Domning (1978), and a fairly diverse cetacean assemblage reported by Barnes (1977). Stratigraphically lower within the Monterey Formation in the same district of Orange County vertebrate fossils, including birds (Howard, 1966, 1968) and cetaceans (Barnes, 1978), have been reported that have closer affinities with Middle Miocene assemblages in California, especially with the Sharktooth Hill Local Fauna in central California. These older assemblages in the Monterey Formation have been correlated indirectly with the earlier part of the Clarendonian land mammal age (Howard, 1978:24).

In the upper part of the Monterey Formation in Laguna Niguel, *Pithanodelphis nasalis* is associated with the gannet, *Morus lompopanus* (Miller, 1925); the booby, *Miosula media* Miller, 1925; the sea cow, *Dusisiren jordani* (Kellogg, 1925a); and the pinnipeds, *Pithanotaria starri* Kellogg, 1925b, and *Imagotaria downsi* Mitchell, 1968, all of which were originally based on specimens from the Late Miocene age diatomites of the Sisquoc Formation near Lompoc, Santa Barbara County, California. This association further reinforces the age yielded by the correlations given above (see also Repenning and Tedford, 1977).

Because the holotype and paratypes of *Pithanodelphis nasalis* were exposed during a construction project as mentioned in the introduction, they were collected in a salvage situation and the precise stratigraphic relationships between them were not recorded. The holotype, LACM 30093, was collected from a fine-grained yellow siltstone bed that was approximately 6 to 8 inches thick and was exposed within a section of otherwise fairly uniformly bedded white diatomite 140 m north of the excavation for the foundation of the main North American Rockwell building. The paratype skull, LACM 26635, was found in a loose, coarse-grained, bed of gray sand uncovered near the northeast corner of the same building. Because the strata in this immediate area generally dip toward the north, the bed that yielded the paratype skull was probably stratigraphically lower in the Monterey Formation than the one that yielded the holotype, but was probably no more than 10 m lower.

The paratype partial skeleton, LACM 29087, was collected from a coarse sand bed within bedded diatomite at the northwest corner of the building, and its stratigraphic position was therefore probably also lower than the holotype. The vertebral column of the paratype was bisected in the thoracic area by machinery that was cutting a trench, and Bohrer and Calhoun independently collected opposite ends of the skeleton. After later conversations with both men I was convinced that only one individual fossil skeleton was involved.

Another partial skull, LACM 123872, and an isolated periotic, LACM 122670, referred to the species were both collected near the base of a very coarse, ca. 3-m-thick bed of yellow sand exposed in a road cut 400 m northwest of the main building site. The sand bed that yielded these fossils has subsequently been observed in the field to lie stratigraphically above the diatomite that produced the holotype, and it is the highest part of the Monterey Formation that is exposed in the vicinity (Barnes, Raschke, and McLeod, in press).

The referred skull, LACM 123873, is from another nearby site, LACM 1101, the same locality that yielded the partial skeleton of an otariid pinniped (LACM 1404) that was identified by Downs (1955) as cf. *Allodesmus kernensis* Kellogg, 1922. This specimen is actually an imagotariine otariid, possibly *Imagotaria downsi* or a closely related species. *I. downsi* is known from such Late Miocene (Clarendonian age) formations in California as the Towsley, Sisquoc, and Santa Margarita (Repenning and Tedford, 1977). The locality (LACM 1101) is 1.4 km from the other Laguna Niguel sites mentioned above that yielded *Pithanodelphis nasalis*, and is separated from them by the wide valley that was formed by Aliso Creek and, thus, no direct stratigraphic correlation is possible. The site is, however, in a well-bedded diatomite very much like that which yielded the holotype skull, and this diatomite is overlain by a coarse yellow sand bed like that which produced the referred specimens of *P. nasalis* at LACM locality 6902. The strata are undoubtedly correlative, and I therefore conclude that all the specimens from these Laguna Niguel localities were collected within the uppermost few tens of meters of the Monterey Formation.

REFERRED SPECIMEN FROM THE MODELO FORMATION. LACM 15196, incomplete skull and jaws with some associated postcranial bones collected from LACM locality 1230, Studio City, Los Angeles County, California, by Terry and Michael Pohl about 1955.

FORMATION AND AGE. Upper Member of the Modelo Formation, Late Miocene age, correlated with the upper part of the Monterey Formation in the San Joaquin Hills (Woodford et al., 1954:fig. 2). The locality is within outcrops of diatomaceous shale that have been mapped as the Upper Member of the Modelo Formation of Late Miocene age (Hoots, 1931). A nearby outcrop of the same rock unit produced the fossil bird, *Sula pohli* Howard, 1958.

ETYMOLOGY. The species name, *nasalis*, is derived from Latin, *nasus*, for nose, and is in reference to the exceptionally large nasal bones of this species.

DESCRIPTION. Skull. The description and reconstructions (Figs. 3, 5, 8) of the skull of *Pithanodelphis nasalis* are composites, being based on all the available skulls. The ho-

lotype is the most complete known skull, but unfortunately it is also the most distorted, the braincase being flattened with the basicranium being pushed to the left side. The paratype skull, LACM 26635, although badly shattered, was not distorted by sediment compaction and exhibits the original proportions of the braincase, thus providing information on the undistorted facial surface and true cranium height. Information on the structure of the zygomatic process, rostrum, and palate was obtained mostly from the holotype (LACM 30093). Both the paratype and holotype yielded data on the squamosal and pterygoid regions. Both of these skulls confirmed the confident identification of the paratype partial skeleton, which includes two skull fragments. The referred skull, LACM 15196, from the Modelo Formation, is the only one with the occipital condyles intact. My restoration of the shape of the pterygoid hamulus and its contained fossa for an air sinus is tenuous. The holotype is crushed obliquely in this area, but it preserves the shapes of the pterygoid-palatine suture, the posterior opening of the sinus and the semicircular notch in the lateral lamina of the pterygoid, and shows that the anterior part of the pterygoid sinus is virtually the same width as the posterior part, and that the hamulus is continuously floored by thin bone. The paratype and holotype skulls both show the relationships between the pterygoid and palatine, and the exposure of the vomer between the pterygoid hamuli.

The sample of skulls includes a range of sizes, with the holotype near the mean (Table 1). The paratype skull, LACM 26635, is the largest and has osteological characters indicative of advanced maturity: its crests, tuberosities and nasal bones are prominent.

Characters that indicate that the small skull referred to the species, LACM 123872, is from a juvenile individual are: small size, short postorbital process of the frontal, incompletely formed vomer on the palate between the pterygoids and a cleft between the frontals on the cranial vertex.

Pithanodelphis nasalis has skull proportions like the living freshwater South American stenine delphinids in the genus *Sotalia* Gray, 1866. The facial surface is roughly square, the rostrum is narrow and of medium length with a broad base, and the braincase is highly vaulted with prominent corners, widely flaring zygomatic processes, and a high vertex.

The premaxillae occupy most of the dorsal rostral surface, have dense surface structure, and on the holotype extend only 7 mm anteriorly beyond the maxillae. They are not fused medially but are closely appressed over the midline of the mesorostral gutter at rostral midlength. The rostral part of each premaxilla is transversely convex, becoming flat-lying posteriorly and nearly vertically oriented at the anterior end. The mid-part of each premaxilla is depressed around the premaxillary foramen, but the medial edge next to the mesorostral gutter is elevated. The premaxillary foramina are situated slightly anterior to the location of the antorbital notches and approximately equidistant between the medial and lateral premaxillary margins. A faint anteromedial sulcus extends anteriorly from each premaxillary foramen and converges toward the medial margin, intersecting it at a point nearly one-third of the distance to the anterior end of the

rostrum. Medial to this faint groove, the surface of the premaxilla is rugose, and this marks the area of attachment of the nasal plug muscle (Lawrence and Schevill, 1956).

A deeper posterolateral sulcus extends posteriorly from each premaxillary foramen, toward the lateral margin of the premaxilla, reaching it at a point over the middle of the orbit. There is only a very faint posteromedial sulcus. Adjacent to the lateral narial margins the spiracular plates are broad, elevated, and convex. The posterior terminations of the premaxillae narrow abruptly and have a slender posterior projection that is constricted between the maxillae and the swollen nasals. This thin projection is only 1 to 2 mm wide and extends about half the remaining distance posteriorly to the occipital crest between the maxilla and nasal.

On the anterior part of the rostrum the lateral surface of the maxilla has a porous texture and presents a nearly vertical surface adjacent to the alveolar row. The maxilla is thicker posteriorly where it forms a squared margin of the rostrum anterior to the antorbital notch and has only a narrow dorsal surface exposure adjacent to the premaxilla. There are three anterior maxillary foramina around the antorbital notches and above the anterior part of the orbit, and one larger posterior maxillary foramen over the posterior part of the orbit. Two or three small foramina exit from the maxillary-premaxillary suture anterior to the antorbital notch.

On the antorbital process the dorsal surface of the maxilla is thin but rugose. Elsewhere on the facial surface the maxilla is smooth, and its margins are elevated medially adjacent to the nasal and posteriorly along the occipital crest. The posteromedial corner of each maxilla extends around the posterior side of the corresponding nasal bone to encroach on the frontal where it is exposed at the cranial vertex. On all of the skulls, the left maxilla does not extend medially as far as does the right one. On the surface of each maxilla is a low, crescent-shaped ridge extending from the area of the posterolateral side of the nasal toward the temporal fossa. Such ridges undoubtedly mark the attachment of one or more of the layers of the nasal musculature (see Mead, 1975), and are most pronounced on the most mature skull (LACM 26635).

The external nares are narrow anteriorly, wide posteriorly, pass vertically into the skull and are separated by a relatively high, thin mesethmoid septum. The right and left narial passages are equal in size and shape. A circular olfactory foramen, approximately 5 mm in diameter in LACM 26635, is located in the center of the posterior wall of each naris. These foramina are the vestiges of a more primitive condition in which the olfactory lobe of the brain had a major connection with the nasal passages. In some primitive fossil odontocetes (e.g., *Zarhachis* Cope, 1868; *Squalodon* Grateloup, 1840; *Argyrocetus* Lydekker, 1894; *Eurhinodelphis* du Bus, 1867) the mesethmoid and ectethmoid bones are distinct and divide the primitively single olfactory fontanelle into two apertures. In Recent delphinids the mesethmoid and ectethmoids are fused into one solid plate and only tiny perforations remain in some individuals and taxa to represent the olfactory foramina (see Kellogg, 1928:199–202). *Pithanodelphis nasalis* demonstrates an intermediate condition in which the mes-

ethmoid and ectethmoids are fused but the olfactory foramina are still relatively large.

There is no prominent suture between the mesethmoid and nasal bones, and the posterior walls of the narial passages merge smoothly with the vertical anterior surfaces of the very bulbous nasals. A large, basin-like depression is on the midline of the anterodorsal surfaces of the nasals. The nasals are separated posteriorly by two vertical, median wedges of the frontals. The frontals are also exposed on the vertex behind the nasals, where they extend as wedges between the nasals and the maxillae, and between the maxillae and the supra-occipital. The nasal bones are proportionally larger than in any other known delphinoid species. On all specimens the left nasal is slightly lower and wider than the right. The suture separating the two nasals bends to the right of the midline of the braincase posteriorly, and the posterior ends of the nasals, therefore, are shifted slightly to the right side of the skull. In derived living odontocetes with asymmetrical cranial vertices, the displacement of the nasal bones is always to the left.

The occipital shield has an unusual conformation for a delphinoid (Fig. 10). The occipital condyles, preserved only on LACM 15196, are separated by a notch ventrally and are relatively small for the skull size (Fig. 8). The occipital crest and the laterally located lambdoidal crests are large and flare posteriorly to outline the occipital shield, which is inclined anterodorsally, has a generally convex surface, and bears a sulcus dorsal to the foramen magnum. The temporal fossae wrap posteriorly around the occipital shield to such an extent that there is no more than a 50 to 60 mm distance between the right and left lambdoidal crests across the posterior surface of the cranium (Fig. 10). The exoccipital is thin, vertically oriented, and flares anterolaterally where it is appressed to the posterior surface of the squamosal. On no specimen is the paroccipital process complete. The posterior side of the right maxilla protrudes farther posteriorly and therefore pushes the occipital shield further posteriorly than does the left maxilla.

The ventral surface of the rostrum is slightly up-curved anteriorly and the palatal surface is generally flat except where it becomes slightly convex posteriorly near the palatine bones. The extent of palatal exposure of the vomer between the maxillae varies in the sample. On the holotype it is about 35 mm long, but on the referred skull LACM 123872 it is 50 mm long. At the anterior end of the exposed vomer the premaxillae appear on the palate medial to the maxillae. They increase in width anteriorly, so that within a distance of 55 mm, the maxillae are entirely excluded from between the alveolar rows.

The largest teeth are in the middle part of the tooth row, where the alveoli are about 5 mm in diameter, and the anterior and posterior ones are progressively smaller. The alveoli are circular with the bone around them raised and rugose. At the anterior rostral extremity, the alveolar rows are very close together. They gradually diverge posteriorly until they are 52 to 55 mm apart at their posterior ends. In specimens with complete tooth rows, the number of upper teeth on each side varies from 27 to 30. In the available

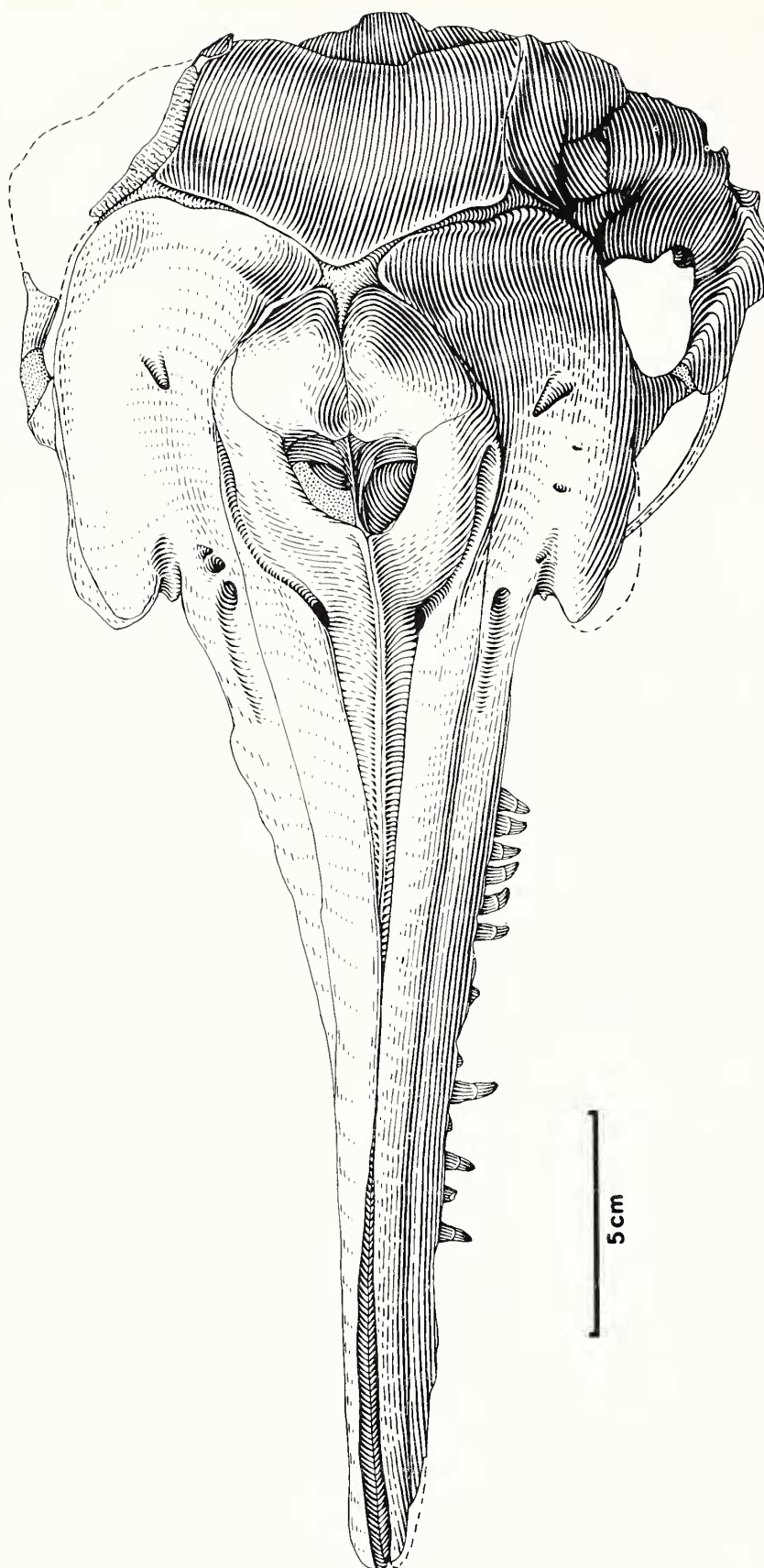


Figure 1. *Pithanodelphis nasalis*, new species, holotype, skull, LACM 30093, LACM locality 5077, dorsal view.

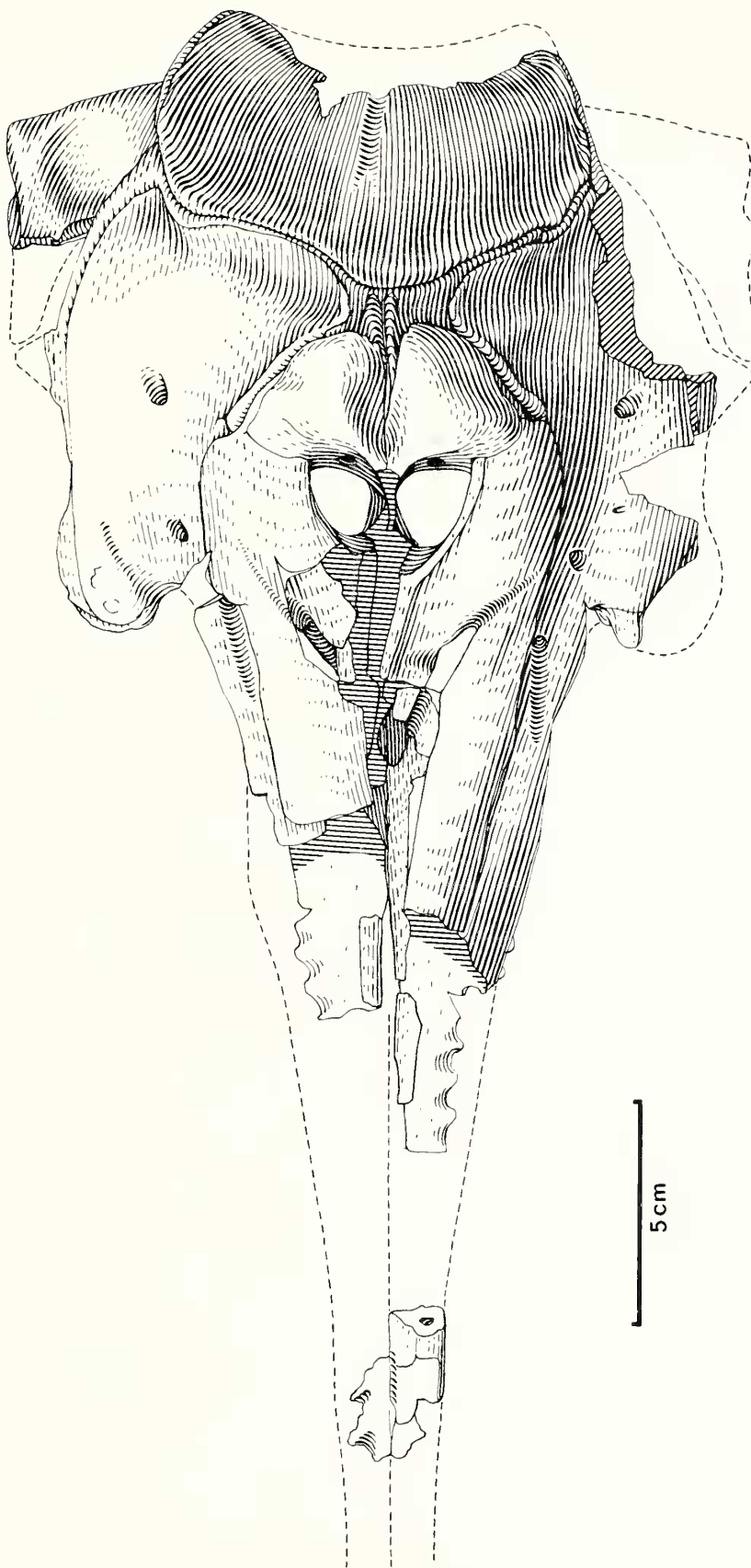


Figure 2. *Pithanodelphis nasalis*, new species, paratype, skull LACM 26635, LACM locality 5069, dorsal view.

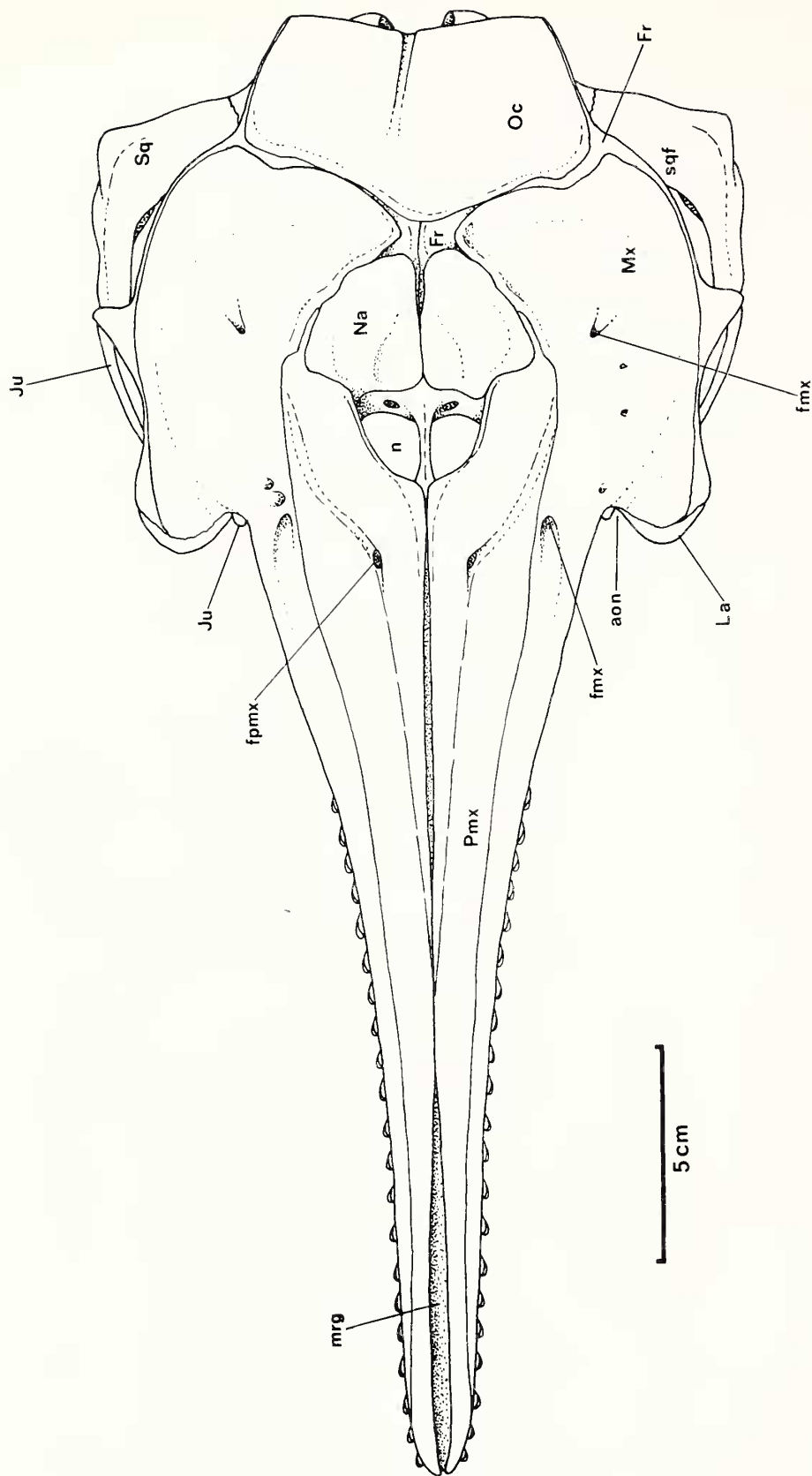


Figure 3. *Pithanodelphis nasalis*, new species, composite reconstruction of skull, dorsal view, based on available specimens; for explanation of abbreviations see Methods and Materials.

sample, the posterior part of the dentition is variable in the following ways. The alveolar row stops at variable distances from the antorbital notch, and this accounts for the above-mentioned variation in the tooth count. In the holotype, LACM 30093, the posteriormost alveoli are significantly smaller than in the paratype, LACM 26635, and in the referred skull, LACM 123872. Some of the specimens show crowding of the posterior teeth, so that in some cases two adjacent alveoli merge.

A palatine foramen in each maxilla near the exposed vomer is confluent with a groove that extends anteriorly and converges on the midline. A larger, less well defined groove on each maxilla originates at the maxillary–palatine suture and extends anteriorly to converge on the midline of the palate. The palatine bones, marked by arc-shaped sutures, extend anteriorly on the palate to a point varying between 14 and 19 mm anterior to the level of the antorbital notches. The maxillae extend posteriorly between the palatines at the midline, between the pterygoid sinus fossae. On the paratype skull (LACM 26635) the vomer descends between the palatines to form a thin, deep keel that extends posteriorly between the nares. The palatines form the sides and roof of the fossae for the pterygoid sinuses, which are shallow, triangular, and pointed anteriorly. Parts of the thin, non-porous pterygoid bone which floored the sinuses are preserved on the holotype skull (LACM 29087). In this area, the bone is very crushed but I can discern a hamular process and a semicircular notch in the lateral lamina of the pterygoid.

The vomer forms a very thin keel separating the nares and it underlies the basisphenoid bone as a thin horizontal plate, extending posteriorly as far as the cranial hiatus. Posterior to this point the basioccipital crest is broken away on all specimens.

Within the orbit there are several foramina. A foramen, elliptical in outline, pierces the lateral wall of the narial passage in the paratype (LACM 26635) and connects with the orbit. The infraorbital foramen is in a position typical of species of Recent Delphinidae—medial to the antorbital notch and near the margin of the pterygoid; but it is smaller, simpler, and not surrounded by struts of bone. The orbital aperture of the foramen is 4 mm in diameter and connects with a branch extending anteriorly within the rostrum to emerge as the premaxillary foramen. Lateral to this, but still confluent with the infraorbital foramen, a smaller foramen connects to the anterior maxillary foramina, and posteriorly another branch leads to the posterior maxillary foramen. A shallow fossa is excavated in the ventral surface of the frontal anterior to, and separated from, the tract of the optic nerve by a thin, elevated crest. This fossa was undoubtedly the location of a small preorbital lobe of the pterygoid air sinus. The sinus did not extend dorsally between the frontal and the maxilla as it does in phocoenids, and, to a lesser extent, in some Recent species of Delphinidae. Another fossa in the frontal bone, posterior to the tract for the optic nerve, marks the site of a postorbital lobe of the pterygoid air sinus (Fraser and Purves, 1960).

The orbit is relatively smaller than in a delphinid such as the Recent common dolphin, *Delphinus delphis* Linnaeus,

1758, but it is still relatively large for a kentriodontid. The antorbital process of the frontal is prominent. The lacrimal bone comprises the anteroventral surface of the antorbital process and its anterolateral part is very thick, but it becomes thin and narrow medially. The lacrimal is wedged into a shallow depression in the ventral surface of the maxilla medial to the antorbital notch. The jugal is fused to the anterior edge of the lacrimal and protrudes into the middle of the antorbital notch, thereby forming a small eminence. This eminence is particularly well preserved on the right side of the holotype (LACM 30093). Such an eminence is unusual for a delphinoid, but a similar one occurs in some species of Recent beaked whales (family Ziphiidae).

The left jugal of the holotype is entirely preserved and appears to retain its approximate original curvature. It measures approximately 80 mm in curvilinear length, is slender and round in cross section anteriorly, and is flattened transversely in its posterior part where it contacts the zygomatic process of the squamosal. It articulates with the squamosal on a small, anteriorly directed process on the ventral margin of the zygomatic process that is in a position similar to that in *Delphinus delphis*.

The temporal fossa is very large, elongate and expanded dorsoventrally. Its anterior part is overhung by the frontal and maxilla. The postorbital process of the frontal is large, tapered, and extends posteroventrally to contact the end of the zygomatic process of the squamosal. Within the posterior part of the temporal fossa the surface of the parietal protrudes laterally. The zygomatic process of the squamosal is large, deep dorsoventrally, and approximately 55 mm long, measuring from the suture with the exoccipital to the anterior extremity. It does not diverge at an angle from the braincase as in most living species of Delphininae, but, more like the monodontids, has its long axis parallel to the midline of the skull. Because the zygomatic process is set far laterally on the cranium, there is a wide squamosal fossa between that process and the lateral wall of the braincase. This squamosal fossa forms a broad and concave floor of the temporal fossa and has a thin and upturned anterior margin.

Distinctive characters of the zygomatic process of *P. nasalis* are its narrow dorsal edge and prominent and square posterolateral corner lateral to the paroccipital process. The latter serves to buttress the glenoid fossa in the area posterior to the nearly vertical postglenoid process. The fossa for the middle air sinus, medial to the glenoid fossa, is partly underhung by a thin, medial extension of the glenoid articular surface for the mandible. A sharp, anteromedially directed crest of bone separates this fossa from the cranial hiatus (which held the ear bones). The homologous crest in most other species of dolphins is developed into the elongate styliform process that descends from the skull, but no indication of such a process is present on any skull of *P. nasalis*. A small foramen (approximately 1 mm in diameter and which can be probed with a needle to a depth of several mm) enters the squamosal dorsal to the position of the external acoustic meatus. The foramen is present on the paratype and holotype of *P. nasalis*, and apparently is characteristic of this species, although its homology and function are unknown. Posterior

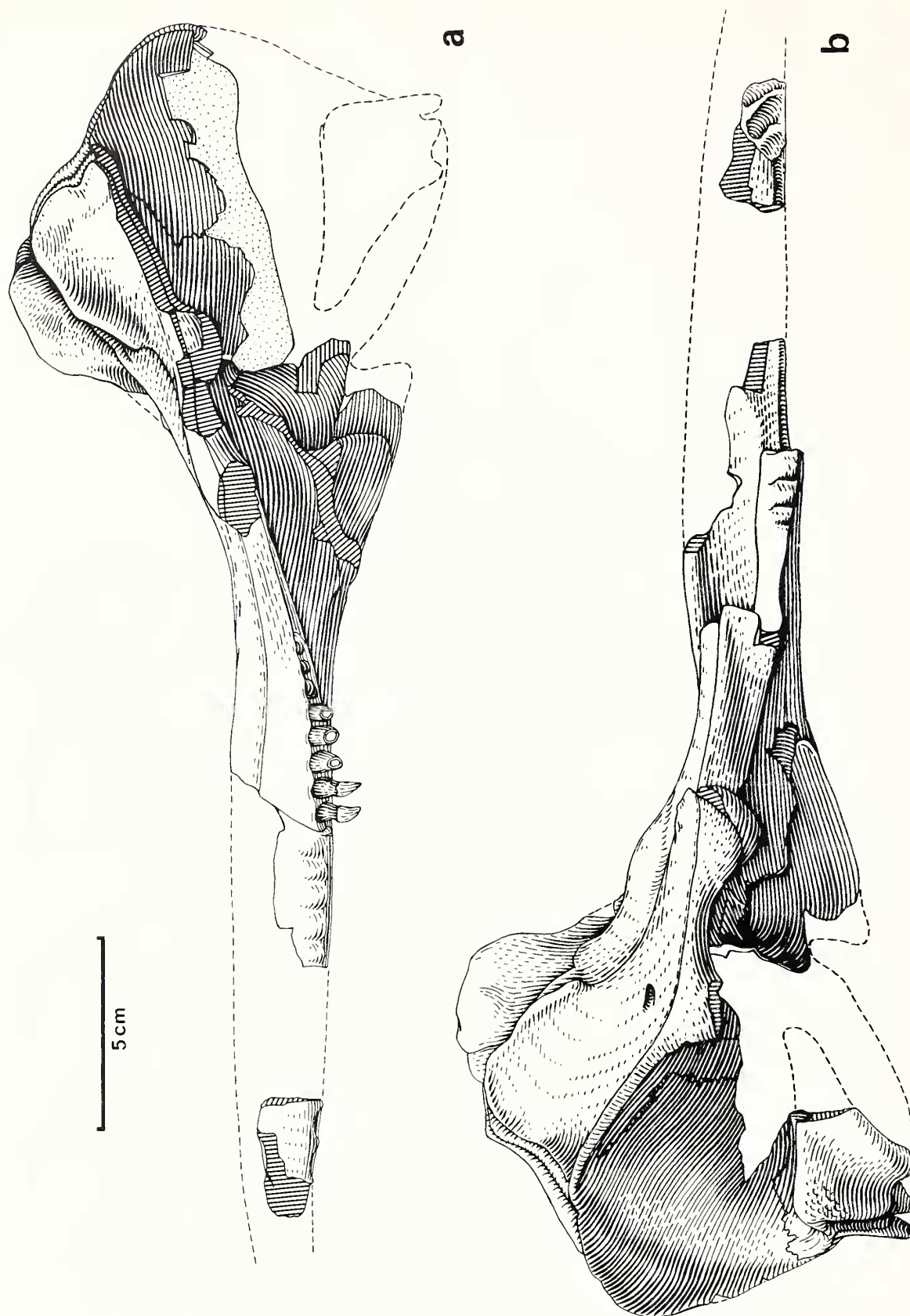


Figure 4. *Pithanodelphis nasalis*, new species, paratype skull, LACM 26635, LACM locality 5069; a, left lateral view; b, right lateral view.

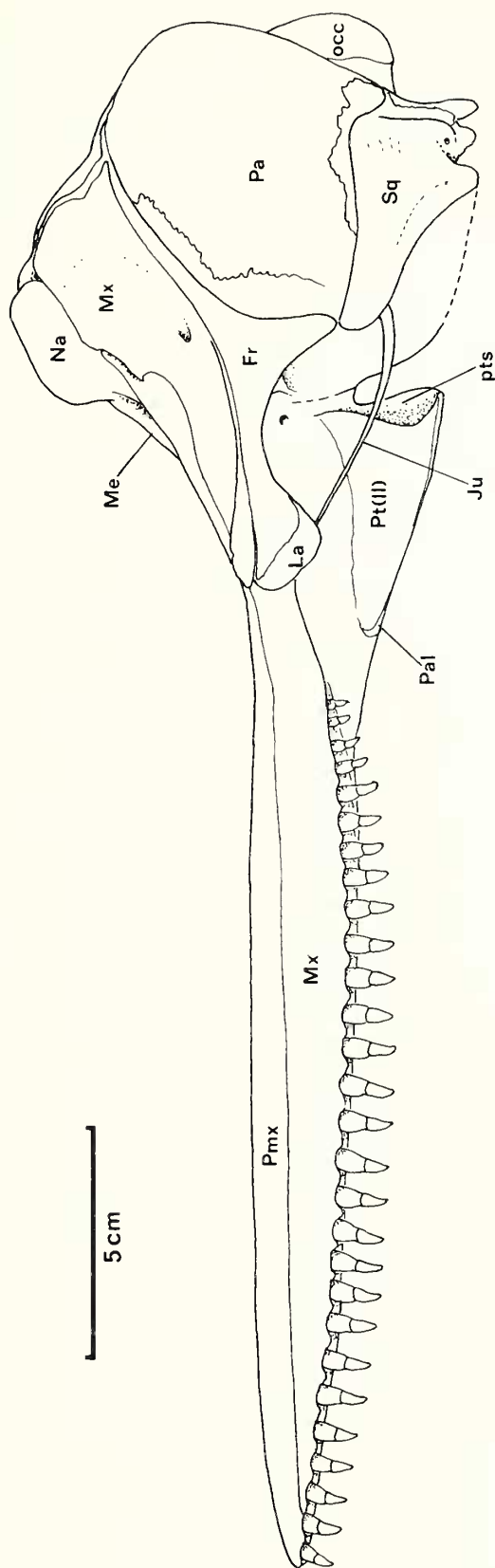


Figure 5. *Pitnanodelphis nasalis*, composite restoration of skull based on available specimens, left lateral view; for explanation of abbreviations see Methods and Materials.

to the glenoid fossa, on the ventral surface of the squamosal, the location of the external acoustic meatus is marked by a broad groove that is oriented transversely. A ventrally projecting part of the squamosal forms the posterior wall of this groove, and is itself separated from the exoccipital by a fissure.

Some ontogenetic changes can be noted within the available sample of skulls. Aside from obvious size increase these include: relative enlargement of the nasal bones and corresponding deepening of the depression between them anteriorly, fusion of the lateral margins of the premaxillae to the maxillae in the area of the spiracular plates around the nares, increase in prominence of the occipital and lambdoidal crests, and increase in thickness of the lateral part of the maxilla anterior to the antorbital notch.

Periotic. One of the two known periotics of *P. nasalis* is the left one from the holotype (LACM 30093). The other (LACM 122670) was found isolated. The cochlear portion of the holotype periotic is crushed in its ventral and medial sections, but the bone is otherwise intact. The periotic of *P. nasalis* is notable by its compact appearance, i.e., the cochlear portion is not prominent, the anterior and posterior processes are small and do not project prominently from the bone, and the whole periotic is somewhat flattened dorsoventrally. In general proportions, absolute size, and relative positions of structures, the periotics of *P. nasalis* somewhat resemble those of an earlier, problematic fossil odontocete, *Lamprolithax simulans* Kellogg, 1931, a species that is known only by isolated periotics from the Middle Miocene age Sharktooth Hill Bonebed in California. These two species show differences of at least generic magnitude, however, and *P. nasalis* has a relatively smaller cochlear portion with a smaller internal acoustic meatus. In *P. nasalis* the cochlear portion is not tilted so much anteriorly and does not have as prominent a crease where it meets the medial surface of the anterior process, the cerebral surface of the periotic lateral to the cochlear portion is smoother and flatter, and the extremity of the anterior process bends dorsally rather than ventrally. Specimens of *L. simulans* (see Kellogg, 1931:figs. 119, 120) have a sinuous, elevated cerebral surface lateral to the cochlear portion, a more distinct and circular fossa for the head of the malleus, and an articular facet for the tympanic bulla which is three-sided, flattened posteriorly, and has an extremity which bends more laterally than posteriorly. In contrast, the periotic of *P. nasalis* has a four-sided posterior articular surface (produced by acquisition of a corner on the lateral edge) and the extremity of the posterior process points posteriorly.

Unusual features of the *P. nasalis* periotic are an eminence on the cochlear portion between the *fenestra rotunda* and the cerebral orifice of *aquaeductus cochleae*, a prominent crest on the posteromedial margin of the internal acoustic meatus, the small size of the meatus, and the small, pointed anterior process. The latter two characters, and the orientation of the meatus, being twisted anteromedially, are similar to the periotic of the holotype of the lophocetine kentriodontid *Lophocetus calvertensis* (Harlan, 1842) (see Barnes, 1978:fig. 1k),

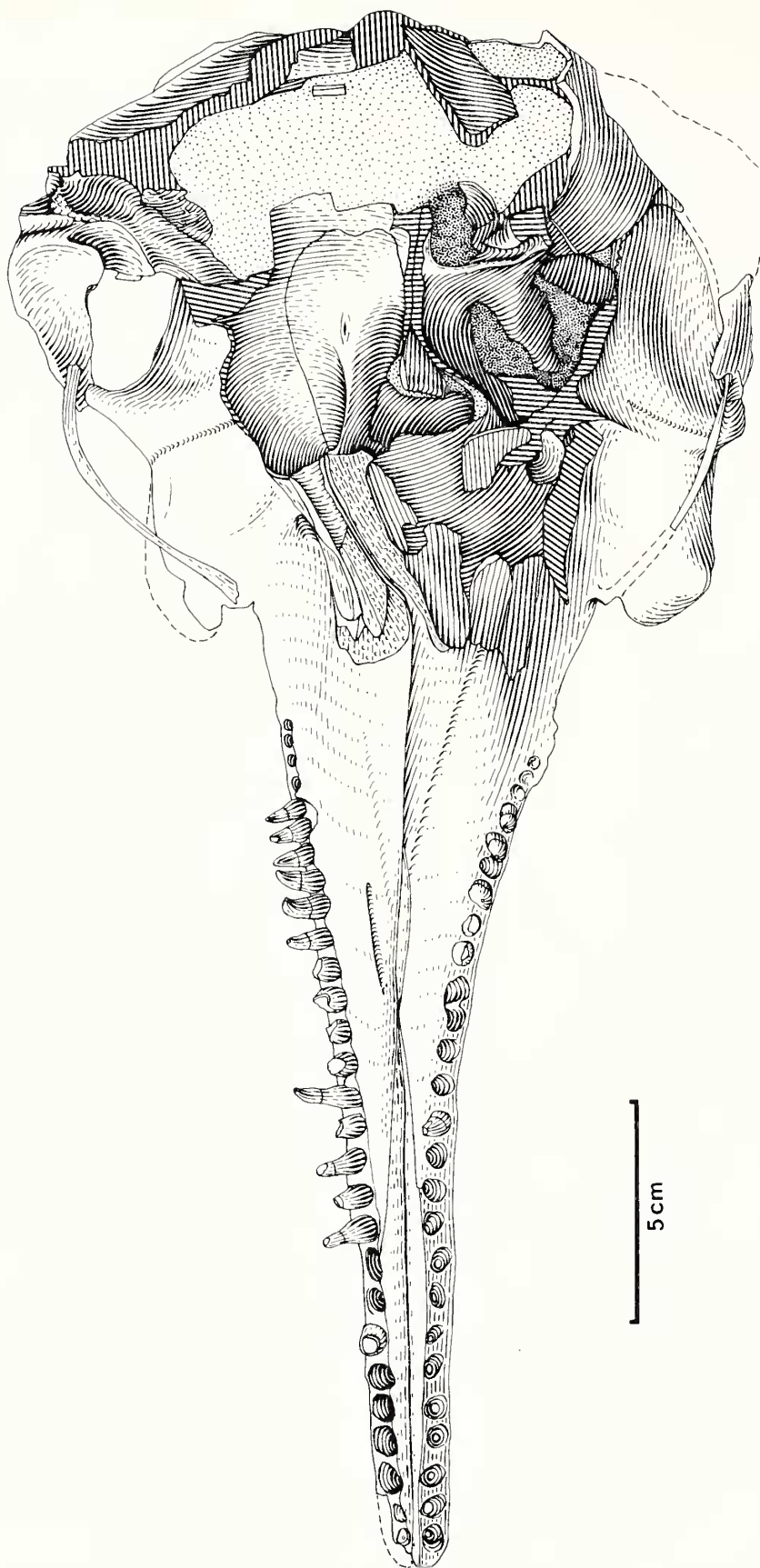


Figure 6. *Pithanodelphis nasalis*, new species, holotype, skull, LACM 30093, LACM locality 5077, ventral view.

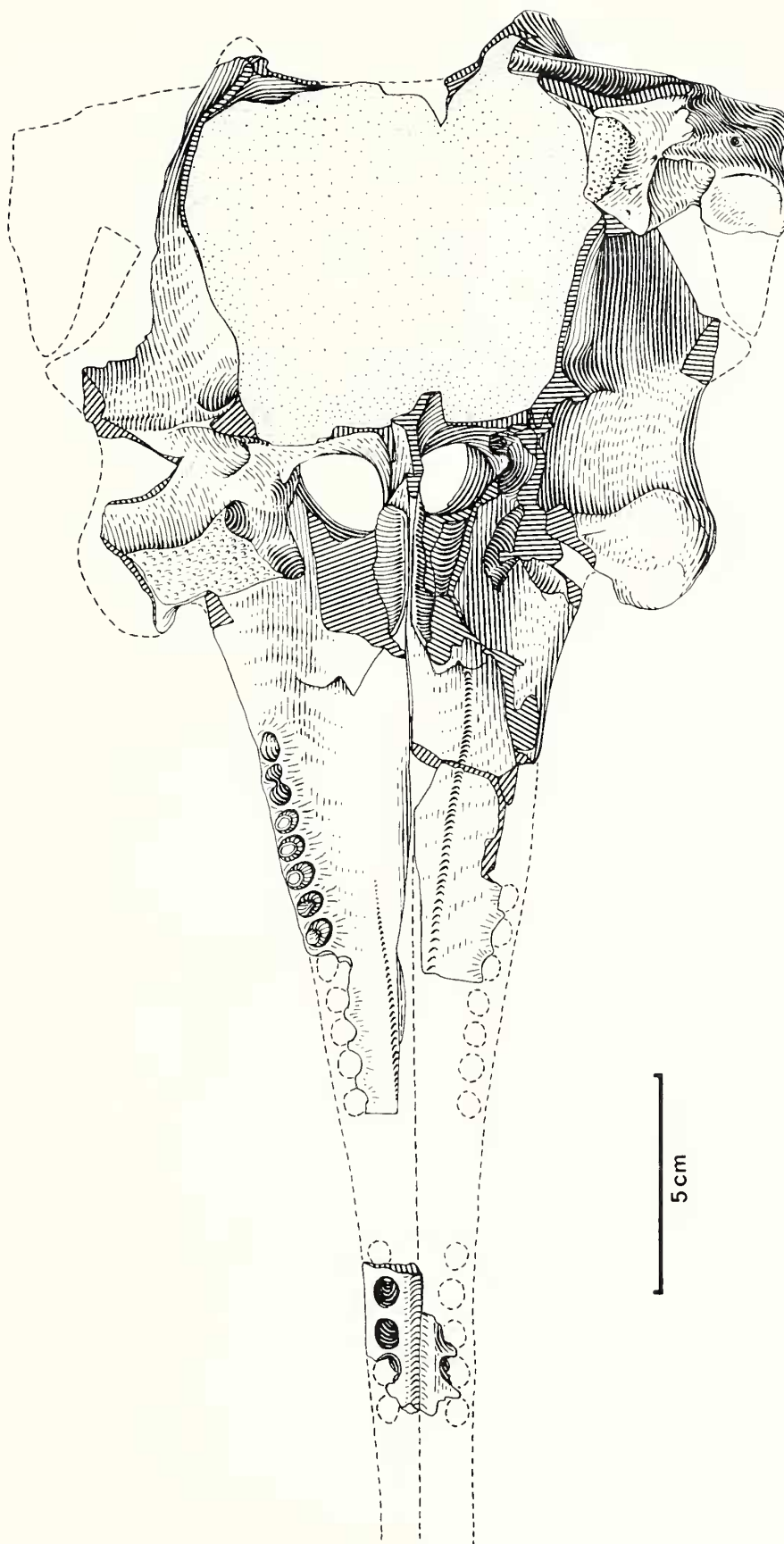


Figure 7. *Pithanodelphis nasalis*, new species, paratype, skull, LACM 26635, LACM locality 5069, ventral view.

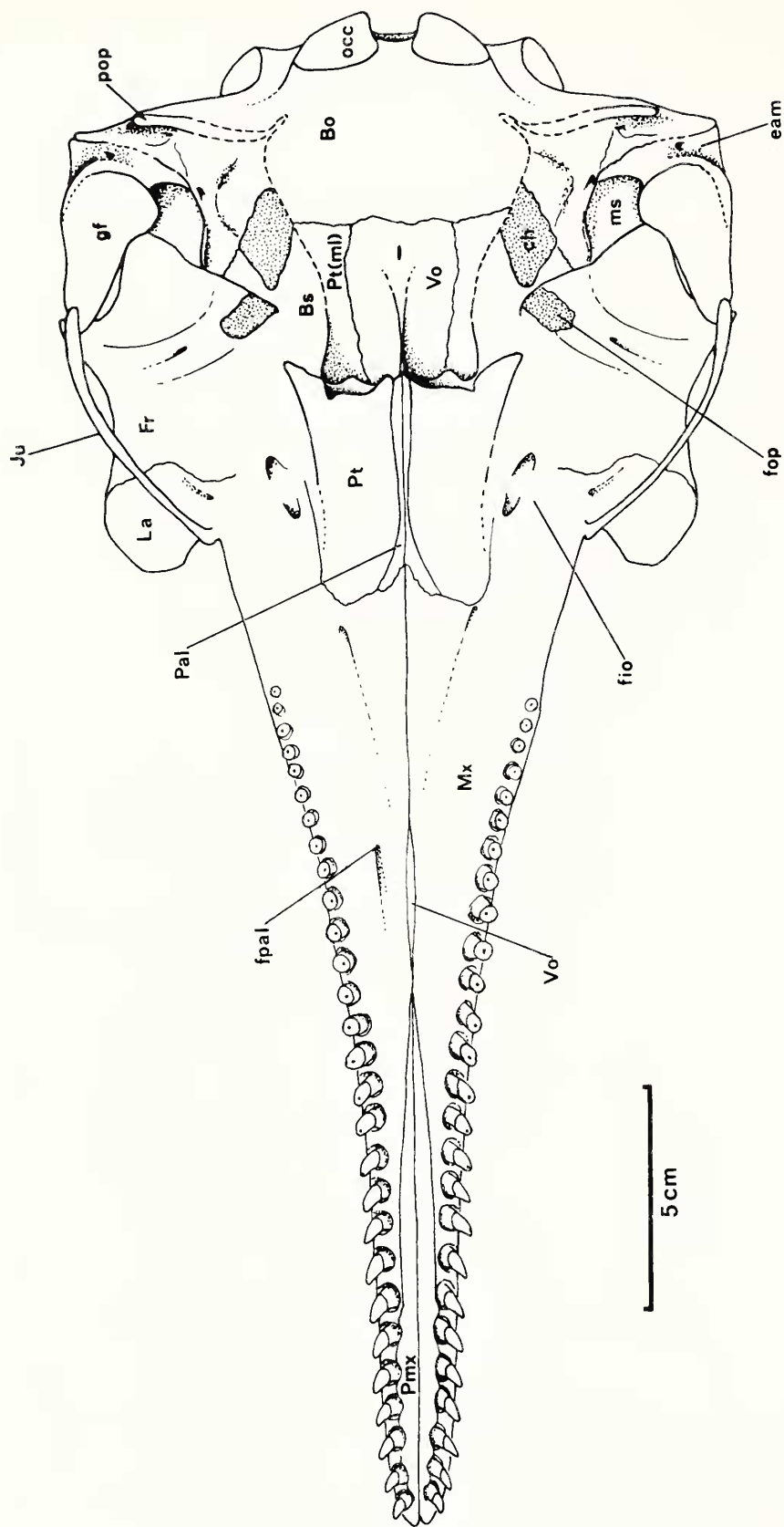


Figure 8. *Pithanodelphis nasalis*, new species, composite reconstruction of skull based on available specimens, ventral view, for explanation of abbreviations see Methods and Materials.

and might indicate some type of evolutionary relationship between *Pithanodelphis* and *Lophocetus* Cope, 1867.

Tympanic bulla. Both tympanic bullae preserved with the holotype are crushed and incomplete. The involucrum is wide and massive compared with living dolphins in the genera *Delphinus* Linnaeus, 1758, or *Stenella* Gray, 1866, and, in its proportions, more resembles those of living porpoises in the genera *Phocoena* Cuvier, 1817, or *Phocoenoides* Andrews, 1911. On the ventral surface of the bulla the posterior end of the involucrum is large and bulbous, the longitudinal groove is broad and shallow, and a transverse constriction separates the anterior and posterior parts. The anterior lip of the bulla is rounded and there is no elongate styliiform process at the aperture of the auditory tube (eustachian tube in part). The sigmoid process is bulbous and the posterior process has an elongate projection posterior to the articular facet for the periotic.

Ossicles. The malleus, incus, and stapes (Figs. 11e–f) were found in the matrix near the left periotic and bulla of the holotype of *Pithanodelphis nasalis*. Ossicles are rarely found and described for fossil cetaceans, but fortunately, the same elements have been described for the holotype of *Kentriodon pernix* (see Kellogg, 1927:28–31, figs. 8–20), and the two species may be compared. The anterior process of the malleus, which in life was fused to the bulla, is incomplete (Fig. 11f), and might have been as large as in *K. pernix*. Compared with *K. pernix*, the tubercle on the malleus of *P. nasalis* is longer and the oblique groove cited by Kellogg is deeper. This groove leads to a foramen (*fovea lateralis*) for the *chorda tympani* nerve that transects the bone from the juncture of the two facets for the incus to the opposite (ventral) side.

The *crus breve* was broken off of the incus. The *crus longum* is shorter and wider than that of *K. pernix*, and the body of the bone has wider articular facets for the malleus. The facet for articulation with the stapes protrudes farther from the side of the *crus longum* than in *K. pernix*.

The stapes of *P. nasalis* differs from that of *K. pernix* by having a larger foramen (intercrustral aperture), a wider head, a more uniformly oval-shaped footplate, a smaller scar for insertion of the stapedius muscle, and a more elongate facet for the incus which is not set so obliquely on the bone.

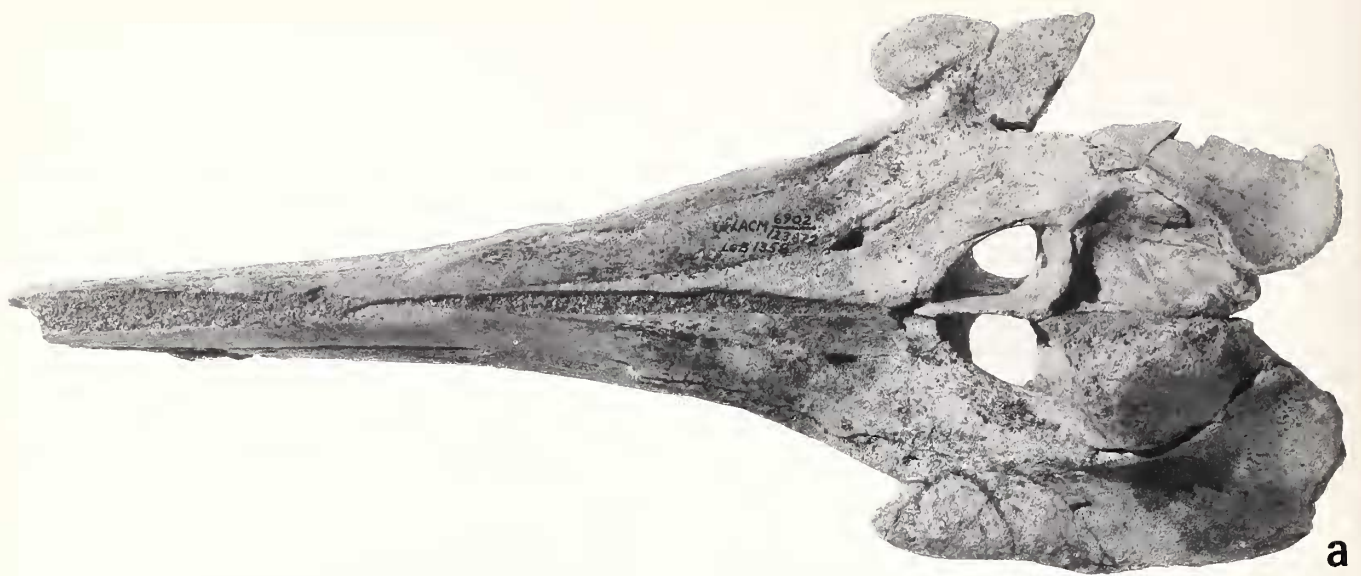
The ossicles have been described for a more distantly related, but contemporaneous fossil delphinoid, the primitive phocoenid, *Salumiphocaena stocktoni* (Wilson, 1973) (see Barnes, 1977, 1984, 1985). That species has a malleus with a wider anterior process and a shorter tubercle, and an incus with a very reduced *crus breve* (Wilson, 1973:figs. 8a–d). Based on comparisons of the ossicles of the three species, *Pithanodelphis nasalis*, *Kentriodon pernix*, and *Salumiphocaena stocktoni*, the former is the most primitive and the latter is the most derived.

Mandible. Some oblique displacement of the right and left dentaries shows that although the two sides were joined by an extensive, rugose symphysis, they were not ankylosed. The symphysis amounts to 40 percent of the length of the mandible. The holotype bears alveoli for 22 teeth in the left dentary, and 21 in the right, of which eight were posterior to the symphysis in the left dentary and seven in the right.

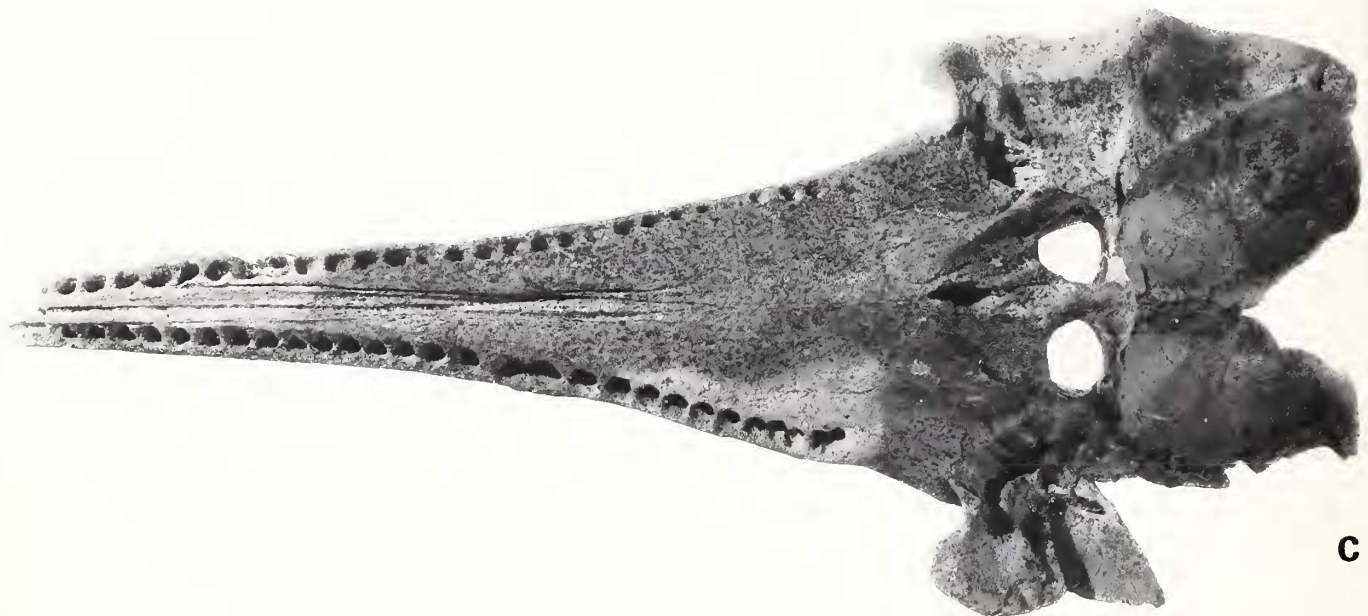
Table 1. Measurements (in mm) of skulls of *Pithanodelphis nasalis*, new species. Parentheses indicate estimated measurements.

	LACM 30093 Holo- type	LACM 26635 Para- type	LACM 123872
Length of rostrum (2)	216	—	185
Width of rostrum at base (3)	78.5	87.5	73
Width of rostrum at midlength (5)	28	—	26
Width of premaxillae at midlength of rostrum (6)	17	—	17
Greatest preorbital width (10)	(127)	(145)	(115)
Greatest postorbital width (11)	(145)	(156)	(115)
Least supraorbital width (12)	125	(138)	112
Greatest width of external nares (13)	33	37.5	33
Greatest width across zygomatic processes of squamosals (14)	(146)	166	—
Greatest width of premaxillae (15)	64.5	80	68
Greatest parietal width, within tem- poral fossae (16)	79	99	—
Length of temporal fossa (19)	(85)	(82.5)	—
Width of temporal fossa (20)	(65)	68.5	—
Length of orbit (25)	(45)	47	—
Length of antorbital process of lac- rimal (26)	20	21	15.5
Length of tooth row (32)	188	—	168
Number of teeth—left tooth row (33)	28	—	30
Number of teeth—right tooth row (34)	26	—	30

The tooth-bearing portion of each dentary is broad dorsally, narrowly keeled ventrally, and bears two or three mental foramina spaced along its lateral surface. The mandible is slender and slightly up-turned anteriorly, and has a deeper, somewhat keeled profile in the posterior symphyseal region. Posterior to the alveolar rows the dentary expands dorsally and ventrally and the bone in this part is thin and more delicate. The posterior end of the coronoid process is directed posteriorly and is separated by a concave mandibular notch from the condyle. A slightly elevated coronoid crest 45 mm posterior to the end of the alveolar row is turned slightly laterally. The angle of the mandible extends farther posteriorly than does the coronoid process, but not farther than the condyle. The condyle has a lateral buttress, is excavated medially, and, when viewed posteriorly, has a vertical medial margin and a convex lateral margin. On the medial surface of the dentary, the anterior margin of the large mandibular foramen extends to about the midlength of the post-symphyseal portion. The opening of this foramen (the mandibular fossa) extends nearly from the dorsal to the ventral margin of the inner surface of the dentary.



5 cm



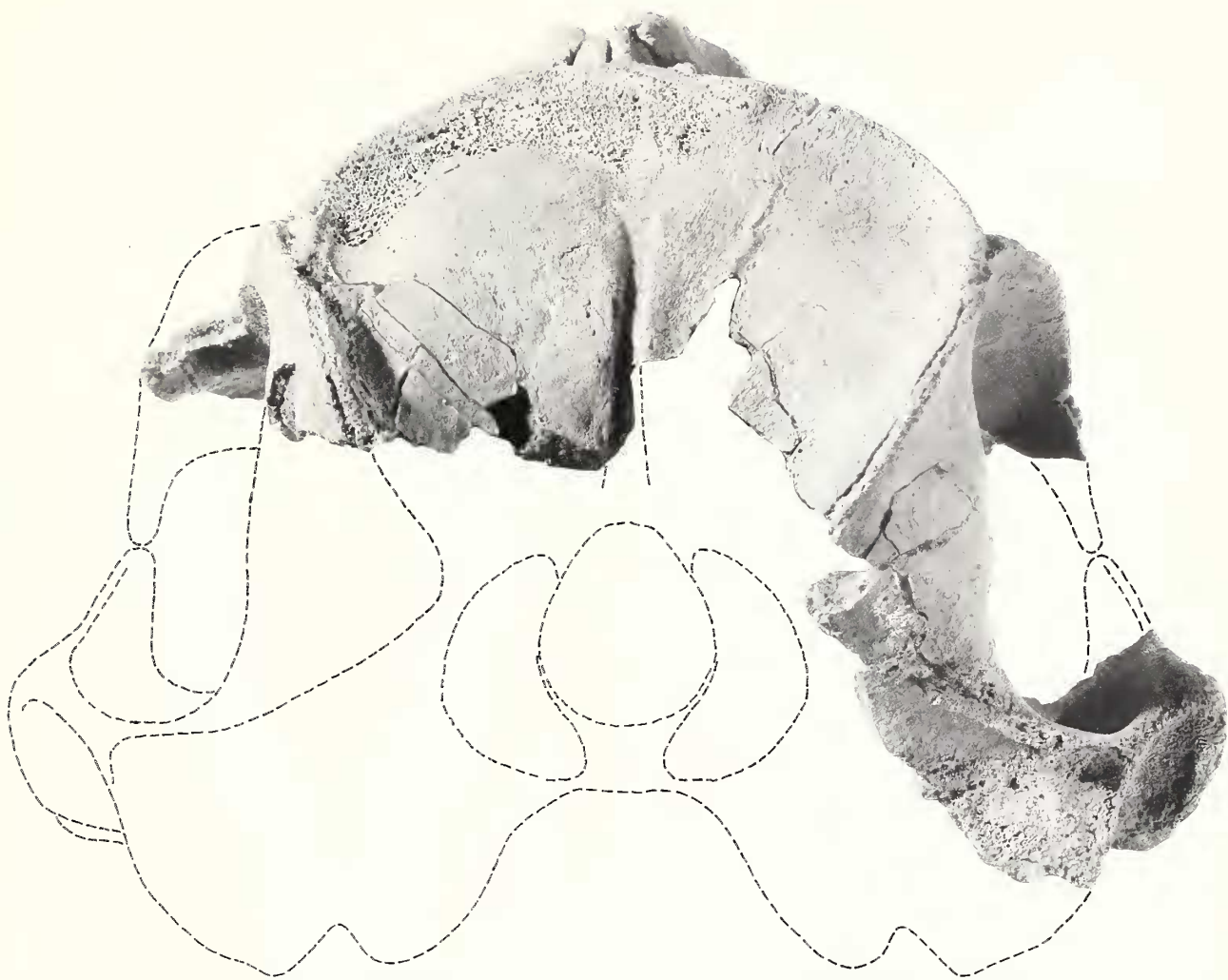


Figure 10. *Pithanodelphis nasalis*, new species, paratype, LACM 26635, LACM locality 5069, posterior view, missing parts indicated by dashed outline, natural size.

In the symphyseal portion of the mandible, the alveolar rows are nearly parallel. They begin to diverge abruptly at the posterior end of the symphysis. Inter-alveolar septa are comprised of cancellous bone and are recessed between prominent labial and lingual borders of the alveolar row. Except for the posteriormost one or two, all of the alveoli are about 4 or 5 mm in diameter and are directed dorsolaterally.

The mandible of *Kentriodon pernix* differs from that of *P. nasalis* by being more slender and more elongate, having a relatively shorter symphysis, a larger mandibular fossa and nearly twice as many teeth. The only known mandible of *Delphinodon dividum*, that of the holotype, is incomplete, missing its anterior end. Compared with *P. nasalis*, it appears to have had a shorter symphysis and it has a higher, less

posteriorly projecting coronoid process, a larger mandibular fossa, and more teeth in that part of each dentary which is posterior to the symphysis.

Teeth. The dental formula on each side in *P. nasalis* is 26–30/21–22. The teeth in the middle parts of both the maxillae and dentaries are approximately 15 mm to 20 mm long, and the anterior and posterior ones are shorter. Each tooth has a smooth, conical, enamel-covered crown that is curved lingually at the apex. Teeth in the anterior and middle parts of the alveolar row have nearly vertical crowns; the more posterior ones have crowns that are shorter and more curved lingually. All crowns bear a proximal lingual bulge that is most prominent on the posterior teeth. The roots taper proximally, bend posteriorly and are bulbous below the gum line (due to added outer layers of cement). No tooth in any of

Figure 9. *Pithanodelphis nasalis*, new species, referred specimen, skull, LACM 123872, LACM locality 6902; a, dorsal view; b, left lateral view; c, ventral view.

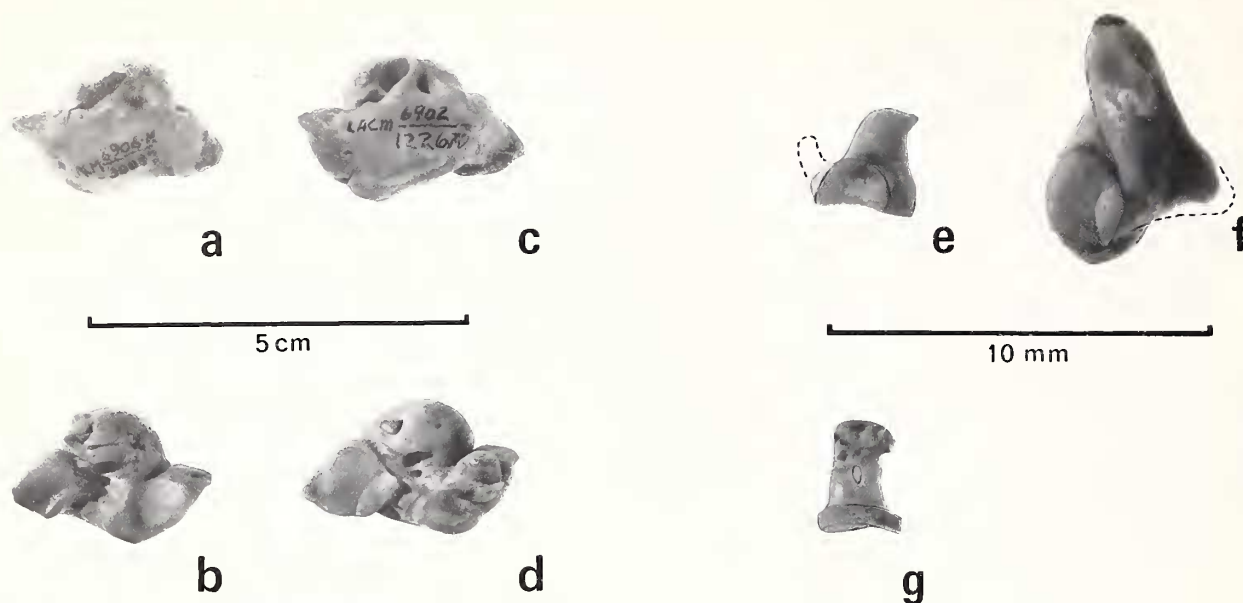


Figure 11. *Pithanodelphis nasalis*, new species, left periotics and ossicles: holotype periotic, LACM 30093, LACM locality 5077; a, cerebral or dorsal view; b, tympanic or ventral view; referred periotic, LACM 122670, LACM locality 6902; c, cerebral or dorsal view; d, tympanic or ventral view; holotype ossicles, LACM 30093, LACM locality 5077; e, malleus, dorsomedial view; f, incus, ventral view; g, stapes, posterior view; a-d, natural size, e-g, $\times 5$.

the skulls shows an open pulp cavity, indicating that the large skulls are all of adults. There is no anteriorly directed, tusk-like premaxillary tooth as in *Kentriodon pernix* (see Kellogg, 1927:pls. 2, 4, 5; Barnes and Mitchell, 1984:fig. 14a).

Vertebrae. The vertebral column of the paratype skeleton (LACM 29087) is not complete, but includes the seventh cervical, the first through sixth thoracic, the last three lumbar, and 25 caudal vertebrae. Apparently there were at least one and possibly two or three additional terminal caudal vertebrae that were not preserved. An unknown number of thoracic and lumbar vertebrae were lost when the skeleton was exposed by a trenching machine.

The spinous processes and the non-rib-bearing transverse processes of these vertebrae are moderately elongate and flat. They are not significantly expanded distally, as is the case in some fossil and living odontocetes (see the unrelated, Recent *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844), for example). The pedicles of the neural arches tilt anteriorly and are positioned anteriorly on the centra. The pedicles of the lumbar and anterior caudal vertebrae are thinner and flatter than those of the thoracic vertebrae. The transverse processes on the thoracic vertebrae are knob-like distally and have shallow foveae for attachment of ribs. At least as far posteriorly in the body as the sixth thoracic vertebra, the capitulae and tuberculae of the ribs were widely separated, judging by the distance between their respective foveae on the vertebrae. The transverse processes of the posterior lumbar and anterior caudal vertebrae are positioned at mid-height on the centra. Starting at the seventh caudal and continuing posteriorly, each vertebra has a vertebral arterial canal on each side, located posterior to the middle of the centrum. Caudals seven through twelve retain spinous and transverse processes, and in each

of these vertebrae the canal pierces the transverse process and is positioned ventral to the posterior edge of the pedicle of the neural arch. After the twelfth caudal, the vertebrae lack spinous and transverse processes, and become progressively more rectangular in shape posteriorly. The eighteenth caudal vertebra is significantly more expanded transversely than the one immediately before it, and has rounded anterior and posterior ends of its centrum. These features indicate that this vertebra was the point of caudal flexion at the anterior margin of the caudal fluke. The vertebrae posterior to this one are expanded transversely. Including the estimated number of missing terminal caudal vertebrae, at least nine vertebrae were originally included within the fluke.

Partial vertebral columns have been described for only two other species of Kentriodontidae; the type specimens of *Kentriodon pernix* (see Kellogg, 1927) and of *Delphinodon dividum* (see True, 1912b). The vertebrae of *Pithanodelphis nasalis* differ from those of *K. pernix* by having spinous processes that are higher and narrower and centra that are more compressed anteroposteriorly and more expanded dorsoventrally. The vertebrae of *Delphinodon dividum* are much more like those of *P. nasalis* in both size and shape. Compared with *P. nasalis*, the spinous processes of *D. dividum* are slightly narrower anteroposteriorly and, in the anterior thoracic region, these processes of *D. dividum* are more nearly vertical and in the anterior caudal region they tilt more anteriorly. The centra of the anterior thoracic vertebrae of *D. dividum* are slightly more compressed anteroposteriorly. Based on these comparisons, the vertebral column of *Pithanodelphis nasalis* is more derived than that of *Kentriodon pernix* and more primitive than that of *Delphinodon dividum*.

At least on the basis of vertebral structure, the living del-

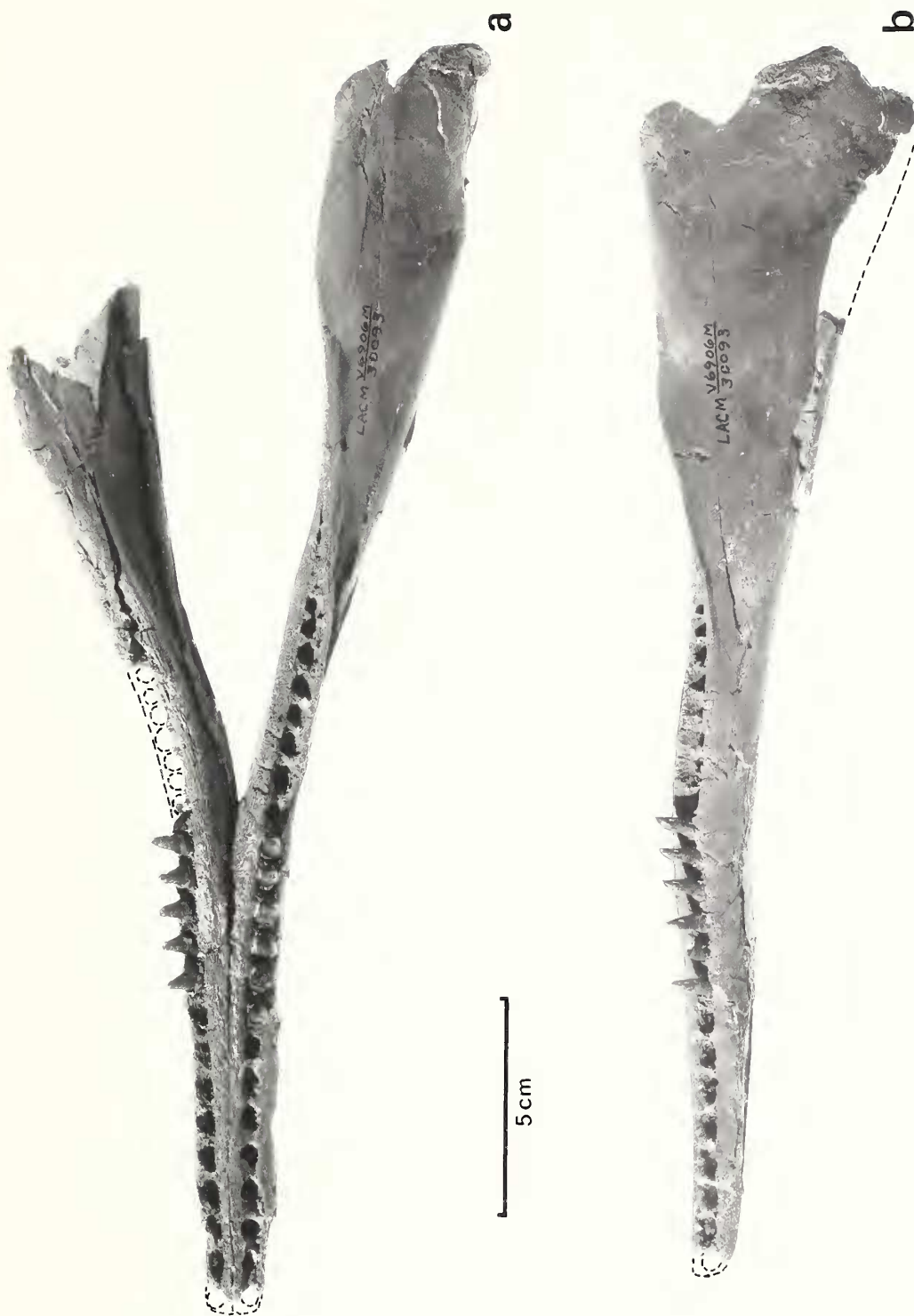


Figure 12. *Pithanodelphis nasalis*, new species, holotype, mandible, LACM 30093, LACM locality 5077; a, dorsal view, b, lateral view of left dentary.

Table 2. Measurements (in mm) of the holotype mandible, LACM 30093, of *Pithanodelphis nasalis*, new species.

Total length of dentary (38)	(298)
Length of tooth row (37)	(170)
Length of symphysis	(120)
Height at coronoid process (39)	66
Length of mandibular fossa (40)	94
Number of teeth—left tooth row (35)	22
Number of teeth—right tooth row (36)	22

phinid species in the genera *Sotalia* and *Sousa* Gray, 1866, are more primitive than *Pithanodelphis nasalis* in having fewer vertebrae, longer centra, and wide, short spinous and transverse processes. The same is true of otherwise relatively derived living species of delphinids such as the pilot whales, *Globicephala* spp.; false killer whales, *Pseudorca crassidens* Owen, 1846; and killer whales, *Orcinus orca* Linnaeus, 1758.

In vertebral shape and proportions, a close living analog of *P. nasalis* is the bottlenosed dolphin, *Tursiops truncatus* Montagu, 1821. Although it is a larger animal, it is useful for interpreting the vertebrae of the fossil. The paratype of *P. nasalis* probably had 26 to 28 caudal vertebrae and individuals of *T. truncatus* have from 26 to 29 (Nishiwaki, 1963). Both species have approximately nine of these caudal vertebrae within the flukes. In *T. truncatus*, the anteriormost caudal vertebra that bears a vertebralarterial canal is the tenth rather than the seventh as in *P. nasalis*. Caudals amount to 36 percent of the vertebral column in *T. truncatus*, and I presume they comprised approximately the same percentage in *P. nasalis* and that the remainder of the vertebrae in the lumbar, thoracic, and cervical regions of the two species are approximately proportional. Based on the measurements of adult skeletons of *T. truncatus*, I calculated that the vertebral column of the paratype of *Pithanodelphis nasalis* (LACM 29087) was approximately 155 cm long. Estimating that it had a skull the length of that with the holotype (LACM 30093), and adding another cm for flesh covering the tip of the rostrum, the probable total body length of the paratype of *P. nasalis* in life was approximately 192 cm. As evidenced by the large paratype skull, LACM 26635, some individuals attained a larger size, and probably reached a total body length of approximately 200 cm.

DISCUSSION

The Late Miocene species *Phocaenopsis cornutus* was first briefly described by du Bus (1872:500), based on two fragmentary skulls from deposits in the Antwerp Basin, Belgium. The genus to which he referred his species, however, *Phocaenopsis* Huxley, 1859, was originally based only on an isolated humerus from New Zealand which Huxley thought was Pleistocene in age. Fordyce (1981) has subsequently shown that the type species of *Phocaenopsis*, *P. mantelli*, is Early Miocene in age and that it belongs either in the family Rhabdosteidae (=Eurhinodelphidae) or Squalodontidae. du Bus (1872:499) had also assigned another fossil species, *Pho-*

caenopsis scheynensis du Bus, 1872, to the same genus, but both of these generic assignments were without sound basis because of the non-comparable nature of the type materials.

Abel (1905:133) transferred *Phocaenopsis scheynensis* to the genus *Acrodelphis* Abel, 1899, and (1905:142) *Phocaenopsis cornutus* to the new genus *Pithanodelphis* Abel, 1905. Abel (1905:140–45, figs. 24–25) identified one of the two skulls described by du Bus as the “original de *Phocaenopsis cornutus*, du Bus.” This is the specimen that I now designate as the lectotype of the species. Abel’s illustrations of the dorsal and right lateral views of the skull and the accompanying text demonstrate the distinctive characters of the species. du Bus had mentioned no other referred bones of this species, but Abel (1905:figs. 26–27) illustrated fused atlas and axis vertebrae that he referred to the species, and in the diagnosis (p. 143) stated that the atlas and axis were nearly always fused, separate only in one example. In my opinion, Abel’s referral of those cervical vertebrae to *Pithanodelphis cornutus* is unfounded, because there are no demonstrated associations with skulls.

The genus *Pithanodelphis* remained monotypic until the present study, and no additional specimens have been referred to the type species. Abel originally classified it in the subfamily Delphininae of the family Delphinidae. True (1912b:192) retained *Pithanodelphis cornutus* in the family Delphinidae and compared it with his new fossil species, *Delphinodon dividum*. Winge (1921) did not contest the familial assignment of *Pithanodelphis*, but did observe that the large medial extensions of the posterior ends of the maxillae behind the cranial vertex was an unusual character when compared with living species in the Delphinidae. (This condition is characteristic of all kentriodontids.) Kellogg (1927) named *Kentriodon pernix* as a new genus and species of delphinid and compared it with *D. dividum*. When Slijper (1936) named the Kentriodontinae as an extinct subfamily of the Delphinidae, he included within it *Kentriodon* and *Delphinodon* and excluded *Pithanodelphis*. Simpson (1945) did not recognize the Kentriodontinae, nor any other extinct or living subfamilies of Delphinidae, but he did list *Delphinodon*, *Kentriodon*, and *Pithanodelphis* among the extinct genera of the family. I recognized the Kentriodontidae as a separate family (Barnes, 1978:25–26), and classified *Pithanodelphis*, *Kentriodon*, *Delphinodon*, and other genera in the nominate subfamily, Kentriodontinae. As a result of the present study, I now recognize substantial numbers of unique, derived features of *Pithanodelphis* that warrant its classification within a separate, new subfamily, the Pithanodelphinae.

I had previously characterized (Barnes, 1978) the family Kentriodontidae, in part, as lacking asymmetry of the cranial vertex, such as exists in all species of Delphinidae (sensu stricto). *Pithanodelphis nasalis* and *P. cornutus* are, however, kentriodontids that do, in fact, have asymmetrical cranial vertices, but the extent of this asymmetry and the ways in which the bones had become modified from the primitive pattern are different from species in the Delphinidae. Among the species of Delphinidae, the pattern of asymmetry and the relationships of the bones that comprise the cranial vertex are very uniform (Barnes, 1978:3), and the unique type of

cranial asymmetry of species of *Pithanodelphis* differs in the following ways. The posterior ends of the premaxillae are the same length instead of the right one being longer. Both premaxillae contact the nasals instead of only one. The posterior end of the right premaxilla adjacent to the nares is only 2 to 4 mm wider than the left instead of being approximately twice as wide. The nasal bones are high and peaked, forming the highest part of the cranial vertex, not low and hemispherical and forming the anterior side of the vertex. The spiracular plates are of equal height, rather than the left being more elevated than the right. The area of the cranial vertex that is occupied by the right and left nasals is equal, rather than the left nasal being smaller. The suture between the two nasal bones twists to the right posteriorly, rather than to the left. The mesethmoid septum between the nares lies on the midline of the skull, instead of being offset to the left side. The nares are equal in diameter, rather than the right being larger.

In *Pithanodelphis*, as in species of Delphinidae, the posterior end of the right maxilla extends farther toward the midline than does the left, and the shapes of the right and left halves of the occipital crest are different. *Pithanodelphis* has additional unique, derived characters that differentiate it from Delphinidae: the left nasal bone is lower than the right, a very slender posterior extension of each premaxilla is compressed between the maxilla and the nasal, and the exposed area of the frontals behind the nasals has a shape with five points.

The cranial asymmetry of *Pithanodelphis* is, therefore, of a different nature than that which is found within the Delphinidae and such asymmetry was probably acquired independently in the two groups from different ancestors that had symmetrical cranial vertices. An as yet unnamed, contemporaneous species of true delphinid, which has an asymmetrical cranial vertex of the type seen in living delphinids, has been found in the same part of the Monterey Formation as *Pithanodelphis nasalis* (see Barnes, 1977). The presence of cranial asymmetry, as well as the well-developed spiracular plates around the nares in *Pithanodelphis*, suggest the presence in life of some type of specialized musculature and nasal passage diverticulae. In living odontocetes such structures have been implicated in production of sound that is used in echolocation (see Mead, 1975).

The retention of a fairly large olfactory fontanelle, as in *Pithanodelphis nasalis*, is primitive and is a relatively uncommon occurrence among other species of fossil odontocetes known after Middle Miocene time. Other primitive cranial characters of the species are the large, laterally placed zygomatic process of the squamosal, the long and tapered postorbital process of the frontal, the exceptionally large temporal fossa and the relatively small fossa for the pterygoid sinus in the pterygoid hamulus. The relatively small size of the paroccipital process is a derived character.

Pithanodelphis might have evolved from some taxon within the subfamily Kentriodontinae because, in addition to the family characteristics, it shares with the earlier Middle Miocene species of *Delphinodon* and *Kentriodon* the following characters: wide facial region, intermediate length rostrum

with premaxilla extending only a short distance anteriorly beyond the maxilla, elongate postorbital process of the frontal, transversely compressed and otherwise similarly shaped zygomatic process of the squamosal, deep squamosal fossa between the zygomatic process and the braincase, similar distribution of air sinuses, and similar sizes and positions of the basioccipital crests and cranial hiatus. *Pithanodelphis nasalis* more specifically shares with *D. dividum*: a slightly arched rostrum, similar tooth count, small paroccipital process, convex lateral margin of the maxilla over the temporal fossa, zygomatic process of the squamosal with tapered anterior end and projecting posterolateral corner, and similar structure and proportions of vertebrae. Teeth without accessory denticles, and the unusually large nasal bones of *P. nasalis* are derived characters compared with *D. dividum*.

Species in the genus *Lophocetus* also have relatively large nasal bones, but these are shaped differently than those of *Pithanodelphis*, being not significantly higher than the maxillae, and more compressed transversely by them. The periotics of both *Lophocetus calvertensis* (see Barnes, 1978:fig. 1k) and *Pithanodelphis nasalis* share an oddly tapered anterior process, a wide lateral portion and a relatively large internal acoustic meatus that is tilted anteriorly on the cochlear portion. It may be that the contemporaneous Late Miocene species of *Pithanodelphis* and *Lophocetus* had closely related Middle Miocene ancestors within the subfamily Kentriodontinae, such as the derived kentriodontine genus *Delphinodon*, and evolved in divergent ways.

Pithanodelphis nasalis and *P. cornutus* are the only species assigned to the genus *Pithanodelphis*. Each species has a different combination of primitive and derived characters. My interpretation of the polarity of these characters is based on the anatomy of much more primitive Odontoceti such as species in the families Agorophiidae, Squalodontidae and in the kentriodontid subfamily Kampholophinae. The more derived characters of *P. cornutus* include its reduced cranial crests and more rounded, convex occipital shield. The derived characters of *P. nasalis* include its larger nasal bones and smaller, more tapered zygomatic processes of the squamosals.

There are very few previously named fossil odontocetes of Late Miocene age from the North Pacific realm (Barnes, 1977), and most are known only by one specimen. In the existing fossil cetacean collections of this age that have been obtained from southern California deposits, however, *Pithanodelphis nasalis* is the most abundant odontocete species and is now represented by seven specimens that are mentioned in this study. This is also the largest published sample of skulls of any kentriodontid species. Such a relatively good sample could, of course, be attributed to a collecting bias, but six of the seven specimens came from a relatively small geographic area in Orange County and from a restricted stratigraphic interval in the Monterey Formation from which virtually all noticeable vertebrate fossils, ranging from single bones to complete skeletons, were collected and prepared. The only specimen of *P. nasalis* recorded in this study that is not from the Monterey Formation in Orange County is from the Modelo Formation in the Santa Monica Mountains of Los Angeles

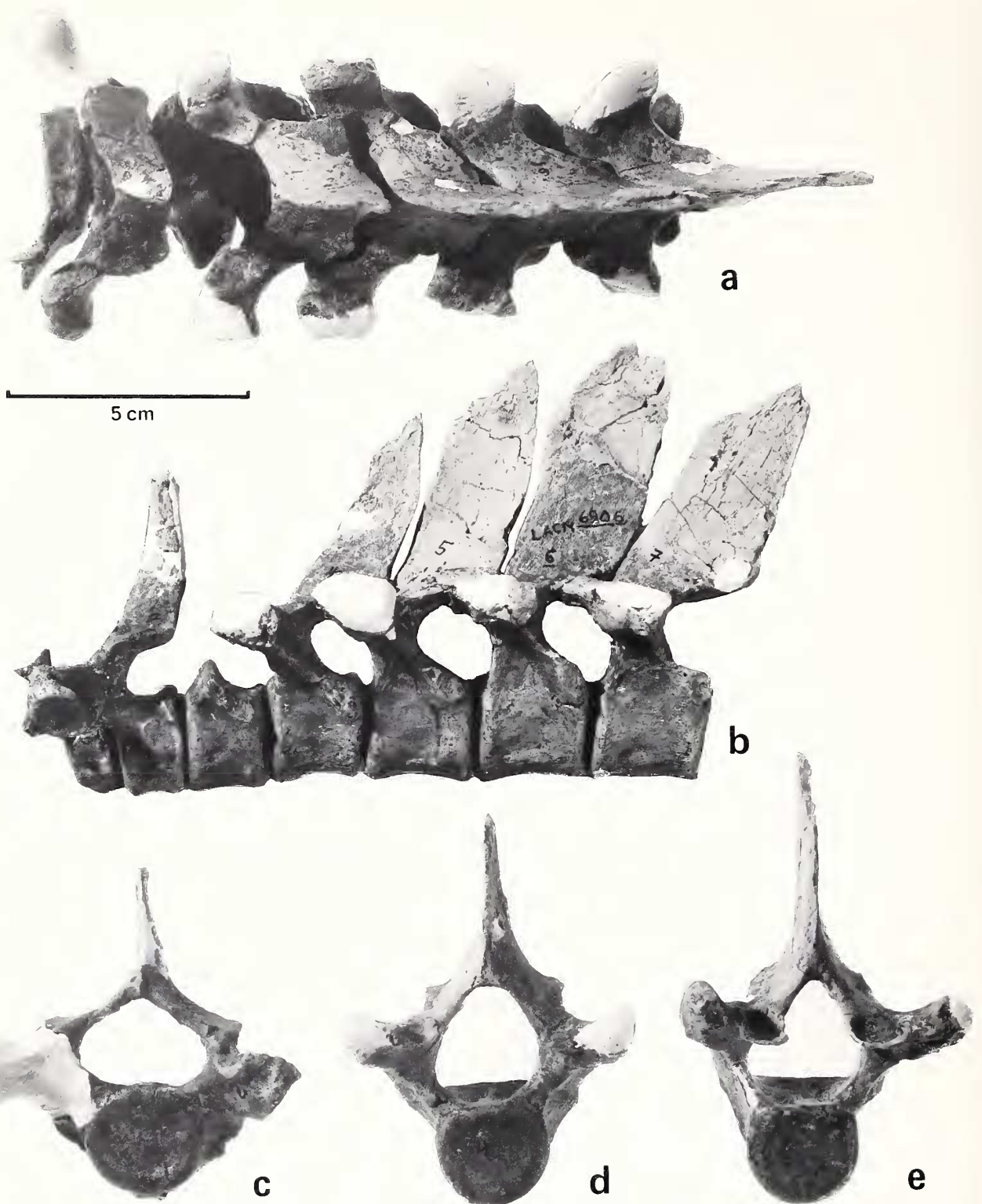


Figure 13. *Pithanodelphis nasalis*, new species, paratype, LACM 29087, LACM locality 5082, cervical and thoracic vertebrae; cervical vertebra 7 through thoracic vertebra 6; a, dorsal view; b, left lateral view; anterior views of individual vertebrae; c, first thoracic; d, third thoracic; e, sixth thoracic. All to the same scale.

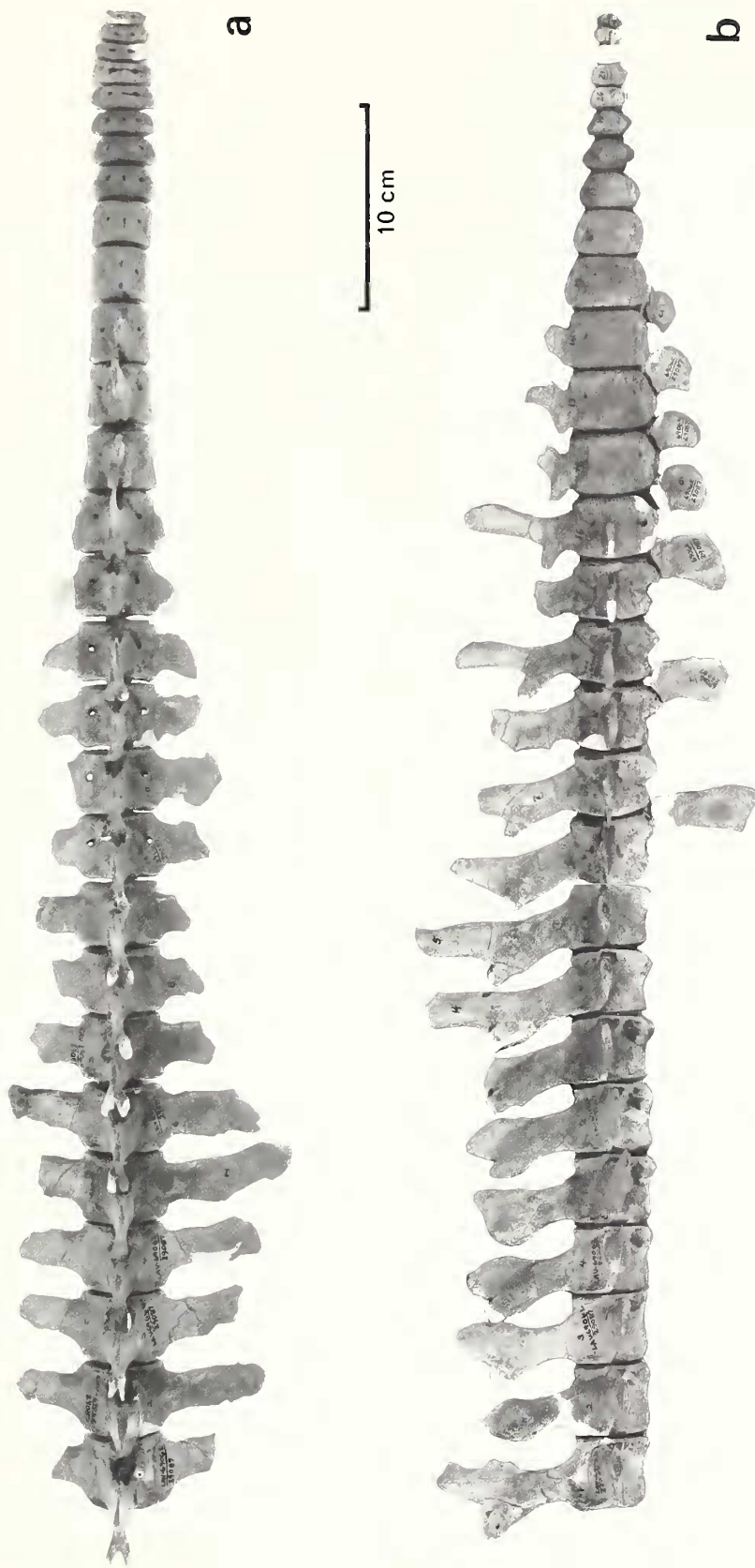


Figure 14. *Pithanodelphis nasalis*, new species, paratype, LACM 29087, lumbar and caudal vertebrae and chevron bones, LACM locality 5082; **a**, dorsal view; **b**, left lateral view.

County. This formation has been correlated with the Monterey Formation in Orange County (Woodford et al., 1954: fig. 2) and because both rock units were deposited in the same marine basin, the Los Angeles Basin, all the specimens may therefore be regarded as part of the same faunal aggregate.

Furthermore, the relatively restricted source of the specimens from the Monterey Formation reinforces the conclusions based on morphological similarities that the specimens attributed to *P. nasalis* represent one species. The sample of skulls presents a range of size, but a consistency of morphology. Within the sample of skulls of *P. nasalis* the variability (in the positions of the premaxillary and maxillary foramina, in the size and shape of the nasals and the antorbital and postorbital processes, and in the size and anterior extent of the fossae for the pterygoid sinuses) is commensurate with that in the small sample of three skulls of the Atlantic kentriodontid, *Kentriodon pernix*, from the Calvert Formation (Barnes and Mitchell, 1984).

Pithanodelphis nasalis was a contemporary of the earliest known delphinid (sensu stricto; see Barnes, 1977:330), which was recovered from the same part of the Monterey Formation at Laguna Niguel. The earliest known phocoenid, *Salumi-phocaena stocktoni* (Wilson, 1973), and two other kentriodontids, *Lophocetus repenningi* Barnes, 1978 and *Liolithax* sp. (see Barnes, 1978), are also known from correlative rock units in California.

Another contemporaneous odontocete, the small dolphin *Delphinus newhalli* Lull, 1914, was collected from the Monterey Formation near Santa Maria, Santa Barbara County, California. It has been classified in the family Delphinidae by Lull (1914) and Simpson (1945), but objectively considered, the present state of preservation and preparation of the holotype and only known specimen preclude its assignment to any particular family (Barnes, 1977:329). *Delphinus newhalli* is a much more derived species than *Pithanodelphis nasalis*. In contrast with *P. nasalis*, it has 40 upper teeth instead of 26 to 30, a more slender mandible with a symphysis approximately one-fourth as long, an edentulous anterior tip of the premaxilla that does not extend beyond the end of the maxilla, and a shorter, thicker zygomatic process of the squamosal that has a more dorsoventrally expanded anterior end.

Hesperocetus californicus True, 1912a, is another contemporaneous dolphin, and is even more problematic. It is known only by a fragment of mandible that was found in the San Pablo Formation in the San Francisco Bay area of California (see Barnes, 1977). It differs from *P. nasalis* by being larger, and by having a thicker mandible with much larger teeth that have rugose, rather than smooth, enamel.

Several lines of evidence suggest that *Pithanodelphis nasalis* was an offshore species that lived in deep water over the continental shelf. Diatomaceous sediments are usually considered to have been deposited in deeper waters over the continental shelves (cf. Calvert, 1966), and all the known fossil occurrences of *P. nasalis* have been found either in such sediments or in lenses of coarser clastic sediment that are enclosed within diatomites. Furthermore, both the San Joa-

quin Hills and Santa Monica Mountains occurrences of *P. nasalis* are at sites that, in Late Miocene time, were many miles out in the marine basin from the inferred ancient shorelines (Woodford et al., 1954). Most of the specimens consist of parts of associated or articulated skeletons or are otherwise relatively unabraded, indicating that they were not transported great distances before their final deposition. Some cetacean carcasses in the modern oceans have been known to drift great distances prior to sinking to the sea floor (Schäfer, 1972:20–21) and it is possible, of course, that the *Pithanodelphis nasalis* fossils represent carcasses that were not buried near the same environment in which they lived. It is undoubtedly significant, however, that all the known specimens have been found in the sedimentary context described above.

Pithanodelphis nasalis had an overall adult body length of approximately 200 cm. The vertebral column has proportions very much like the living bottlenosed dolphin, *Tursiops truncatus*. Its rostrum and teeth are also like that species and other small living delphinids, and by analogy, its diet was probably generalized, consisting mostly of small pelagic fish and some squid (Rice, 1984:479). Such a diet would also be consistent with the inference that *P. nasalis* was an offshore species. *Pithanodelphis nasalis* was also a generalized animal in its postcranial, mandibular, and dental morphology. Its cranial asymmetry, moderate development of fossae for air sinuses, and large mandibular fossa suggest that it was capable of echolocating. The orbits are relatively large compared with *Kentriodon pernix*, indicating that *P. nasalis* had large eyes. The teeth are large and deeply rooted. The largest teeth are in the middle of the tooth row, and all teeth have a considerable accretion of cementum on their roots. The large temporal fossa indicates that there was strong temporal musculature, which, in conjunction with the large teeth, long, firmly ankylosed mandibular symphysis and large postglenoid process, suggests that *P. nasalis* could effect a strong grasp with its jaws.

CLASSIFICATION

The classification presented below reflects the changes in knowledge of the family Kentriodontidae subsequent to my 1978 publication and includes the taxa that were discussed by Barnes and Mitchell (1984). Within genera, the more primitive species are listed first, and in general, I follow this arrangement throughout the classification. Certain aspects of the anatomy of *Leptodelphis stavropolitanus* Kirpichnikov, 1954, *Sarmatodelphis moldavicus* Kirpichnikov, 1954, and *Microphocaena podolica* Kudrin and Tatarinov, 1965, are poorly known, and it is difficult to assign these genera to established subfamilies. The new subfamily Pithanodelphinae reflects the very derived characters of *Pithanodelphis*, including the asymmetry of the cranial vertex, which is not known among other species of Kentriodontidae and which was acquired in a manner unlike that in other families within the superfamily Delphinoidea. *Oligodelphis azerbaijanicus* was classified by Mchedlidze (1976) as a species of Delphinidae, but appears to belong in the Kentriodontidae, and should therefore be re-evaluated in detail.

Class Mammalia Linnaeus, 1758
 Order Cetacea Brisson, 1762
 Suborder Odontoceti Flower, 1867
 Superfamily Delphinoidea (Gray, 1821) Flower, 1864
 Family Kentriodontidae (Slijper, 1936) Barnes, 1978
 Subfamily Kampholophinae Barnes, 1978
Kampholophos Rensberger, 1969
Kampholophos serrulus Rensberger, 1969.
 Middle Miocene, California, U.S.A.
Liolithax Kellogg, 1931
Liolithax pappus (Kellogg, 1955) Barnes,
 1978. Middle Miocene, Maryland,
 U.S.A.
Liolithax kernensis Kellogg, 1931. Middle
 and Late Miocene, California, U.S.A.
Liolithax sp. Barnes, 1978. Late Miocene,
 California, U.S.A.
 Subfamily Kentriodontinae Slijper, 1936
Kentriodon Kellogg, 1927
 aff. *Kentriodon*. Barnes and Mitchell, 1984.
 Early Middle Miocene, California,
 U.S.A.
Kentriodon pernix Kellogg, 1927. Middle
 Miocene, Maryland, U.S.A.
Kentriodon obscurus (Kellogg, 1931) Barnes
 and Mitchell, 1984. Middle Miocene,
 California, U.S.A.
Delphinodon Leidy, 1869 (in part)
 aff. *Delphinodon dividum* True, 1912b. Barnes
 and Mitchell, 1984. Late Early and/or
 Early Middle Miocene, Japan; Califor-
 nia, U.S.A.
Delphinodon dividum True, 1912b. Middle
 Miocene, Maryland and Virginia, U.S.A.
 Subfamily Lophocetinae Barnes, 1978
Lophocetus Cope, 1868
Lophocetus repenningi Barnes, 1978. Late
 Miocene, California, U.S.A.
Lophocetus calvertensis (Harlan, 1842) Cope,
 1868. Late Miocene, Maryland, U.S.A.
 Subfamily Pithanodelphinae, new subfamily
Pithanodelphis Abel, 1905
Pithanodelphis nasalis, new species. Late
 Miocene, California, U.S.A.
Pithanodelphis cornutus (du Bus, 1872) Abel,
 1905. Late Miocene, Belgium
 Kentriodontidae, *incertae sedis*:
Oligodelphis Mchedlidze and Aslanova in
 Mchedlidze, 1976
Oligodelphis azerbaijdzanicus Mchedlidze and
 Aslanova in Mchedlidze, 1976. Late
 Oligocene, Azerbaidzhan S.S.R.,
 U.S.S.R.
Sarmatodelphis Kirpichnikov, 1954
Sarmatodelphis moldavicus Kirpichnikov,
 1954. Late Miocene, Moldavian S.S.R.,
 U.S.S.R.
Leptodelphis Kirpichnikov, 1954

Leptodelphis stravropolitanus Kirpichnikov,
 1954. Late Miocene, Stavropol, Russian
 S.F.S.R., U.S.S.R.
Microphocaena Kudrin and Tatarinov, 1965
Microphocaena podolica Kudrin and Tatar-
 inov, 1965. Late Miocene, Ukrainian
 S.S.R., U.S.S.R.

CONCLUSIONS

Pithanodelphis nasalis is a new species of small fossil dolphin classified in the new subfamily Pithanodelphinae of the extinct delphinoid family Kentriodontidae. The species is known by fossil skulls and postcranial bones from the Monterey and Modelo formations at about 33°30' and 34°05' north latitudes, respectively, in the Los Angeles Basin in southern California, U.S.A. Its abundance in collections suggests that this dolphin was the most abundant odontocete cetacean inhabiting the North Pacific Ocean off the coast of southern California at approximately 10 to 11 million years ago. The fossil material is sufficient to confidently differentiate *P. nasalis* from previously named, contemporaneous small odontocetes from California: *Hesperocetus californicus* True, 1912a; *Delphinavus newhalli* Lull, 1914; *Salumiphocaena stocktoni* (Wilson, 1973); and *Lophocetus repenningi* Barnes, 1978.

Pithanodelphis nasalis and *P. cornutus* (du Bus, 1872), an approximately contemporaneous fossil species that was found in the Antwerp Basin in Belgium, are the only species presently assigned to the genus and to the subfamily Pithanodelphinae. *Pithanodelphis* might have evolved from some taxon within the subfamily Kentriodontinae. *Pithanodelphis nasalis* is similar to two well-known Middle Miocene Atlantic kentriodontines, *Kentriodon pernix* Kellogg, 1927, and *Delphinodon dividum* True, 1912b. Its vertebral structure is more derived than that of the former, more primitive than that of the latter, and its cranial structure is more derived than both. Species of *Pithanodelphis* differ notably from all other delphinoids by having extremely large, convex nasal bones that comprise the highest part of the cranial vertex.

Pithanodelphis nasalis and *P. cornutus* are the only species of Kentriodontidae that are known to have had cranial asymmetry. The manner in which this asymmetry was expressed is different, however, from species in the other families of the superfamily Delphinoidea; the Monodontidae, Phocoenidae, and Delphinidae; and this feature is, therefore, a convergent derived character. Asymmetry was possibly acquired separately in each of the modern delphinoid families (and in other odontocete families as well).

The presence of cranial asymmetry and other derived characters of *Pithanodelphis nasalis*, such as spiracular plates on the premaxillae, moderate development of fossae for air sinuses in the basicranium, and large mandibular fossae, suggest that the species could echolocate. It has a rostrum of moderate length and a homodont dentition comprised of conical-crowned teeth. Like most small Recent delphinids with such features, it probably had a generalized diet consisting mostly of small fishes and occasional squid. The mor-

phology of its vertebral column is relatively primitive and, in conformation and numbers of vertebrae, is approximately analogous to that of the living bottlenosed dolphin, *Tursiops truncatus*. *Pithanodelphis nasalis* was a smaller animal, however, with an overall body length at maturity of approximately 200 cm. The nature of the sedimentary deposits that yielded the fossils and the preservation of the bones indicate that the usual habitat of the species was probably offshore in deep water over the continental shelf.

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